Vol. V October, 1932 No. 2c.

BULLETIN

OF

THE NEW YORK STATE COLLEGE OF FORESTRY
AT SYRACUSE UNIVERSITY
HUGH P. BAKER, *Dean*

Roosevelt Wild Life Annals

VOLUME 3 NUMBER 2

OF THE

Roosevelt Wild Life Forest Experiment Station

PARASITES OF ONEIDA LAKE FISHES

PART 2. *Descriptions of New Species and some general taxonomic considerations, especially concerning the Trematode Family Heterophyidae*

Trichodina renicola (Mueller, 1931), a ciliate parasite of the urinary tract of Esox niger

CONTENTS OF RECENT ROOSEVELT WILD LIFE BULLETINS

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Entered as second-class matter October 18, 1927, at the Post Office at Syracuse, N. Y., under the Act of August 24, 1912

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PARASITES OF ONEIDA LAKE FISHES

PART II. DESCRIPTIONS OF NEW SPECIES AND SOME GENERAL TAXONOMIC CONSIDERATIONS, ESPECIALLY CONCERNING THE TREMATODE FAMILY HETEROPHYIDAE.

By Justus F. Mueller* and Harley J. Van Cleave †
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INTRODUCTION

Four years ago the authors undertook an investigation of the parasites of the fishes of Oneida Lake, New York, as a part of the program of the Roosevelt Wild Life Station. It was hoped that an intensive study of parasites in a single lake might yield valuable information on the numerous and complicated problems of host-parasite relationships. Before any analysis of our results could be made available and the reciprocal relations of host and parasite could be discussed in terms of ecological and biological relationship, it was necessary to make accurate identifications of extensive collections of parasitic worms. The scattered condition of the literature and the unsatisfactory descriptions available for many of the species have rendered identifications difficult. In spite of the fact that fish parasites have been studied rather intensively on this continent for two generations, we have continued to encounter new species which can be discussed in their relations to the biology of fishes, and the life of the lake as a whole, only after they have been named and described and their proper positions in the general scheme of classification have been determined.

In Part I of our survey (Van Cleave and Mueller, 1932), we presented descriptions of twelve species of trematodes and three species of nematodes which we considered as new. The species included in the foregoing article comprised forms encountered in the first two years of our field investigation. Collections taken during the summer of 1931 have yielded a considerable number of parasitic worms not previously found in the lake as well as better specimens of some of the species obtained in previous summers. Among these new records there are included nine new species of parasitic worms for which descriptions are presented for the first time in this paper. The descriptions of species in both Parts I and II are but preliminary to the initial object of the survey,—a final report which will include observations on the biology and ecology of the worm parasites of Oneida Lake fishes. Since the collections herein considered are but continuations and extensions of the field and laboratory studies initiated in Part I of this report, the acknowledgments of personal and professional obligation extended in Part I are implied without repetition.

There are four fairly distinct sections of the present paper. In Section 1 are assembled the specific descriptions of nine new species of parasitic worms. These include seven trematodes or flukes, one cestode or tapeworm, and one nematode or roundworm. The following list gives the names of the nine new species here described.

New species of flukes or Trematoda

Family Heterophyidae

Allacanthochasmus artus

Family Allocreadiidae

Allocreadium halli
Triganodistomum attenuatum
Triganodistomum simeri

FAMILY STRIGEIDAE

Neascus grandis

FAMILY GYRODACTYLIDAE

Gyrodactylus cylindriformis

Dactylogyrus extensus

New species of tapeworm or Cestoda

FAMILY PTYCHOBOTHRIIDAE

Bothriocephalus formosus

New species of roundworm or Nematoda

FAMILY TRICHINELLIDAE

Hepaticola bakeri

In addition to the descriptions of new species, a number of general taxonomic problems are discussed. Two species of nematodes belonging to the genus Spinitectus, encountered in our survey, fail to agree with the descriptions of known members of the genus but the points of difference have been determined as resulting from incomplete and in some extent erroneous descriptions of species. These two species of Spinitectus are here redescribed and accurately differentiated for the first time as Section 2 of this paper.

In connection with our extended field study of living worms and laboratory investigation of preserved specimens, we have had unusual opportunity for understanding the morphology and taxonomy of some of the forms studied, because of the relative abundance and excellent condition of the material at our disposal. Among the trematodes parasitic in fishes, there are several genera which have been the subject of disputed relationships by investigators specializing on the taxonomy of this class. Several of these genera of uncertain family affiliations have been so favorably represented in our collections that we are able to offer conclusive evidence of their relationship which align them directly with the family Heterophyidae. One section of this paper (Section 3) sets forth the detailed evidence which has led us to place the genera Vietosoma, Acetodextra, Allacanthochasmus, Neochasmus, Caecincola, Cryptogonimus and Centrovarium in the family Heterophyidae. At the same time, we have reviewed the old arguments and have amassed new information on the family relationships of members of the genus Microphallus which has frequently been assigned to the Heterophyidae. On the basis of detailed evidences set forth in Section 4 of this paper, Microphallus is excluded from the Heterophyidae and, following the recommendation of Travassos (1920), is recognized as type of the family Microphallidae.

In the section which immediately follows, the description of each new species is preceded by a brief statement of its systematic position.

Plate 15. *Allacanthochasmus artus* new species.

Fig. 1: A young, mature specimen of *Allacanthochasmus artus* seen from dorsal surface.

Fig. 2: An oral spine of *A. artus,* in lateral view, for comparison with Fig. 3. Stippled portion of spine embedded in oral sucker. Outline of oral sucker stippled.

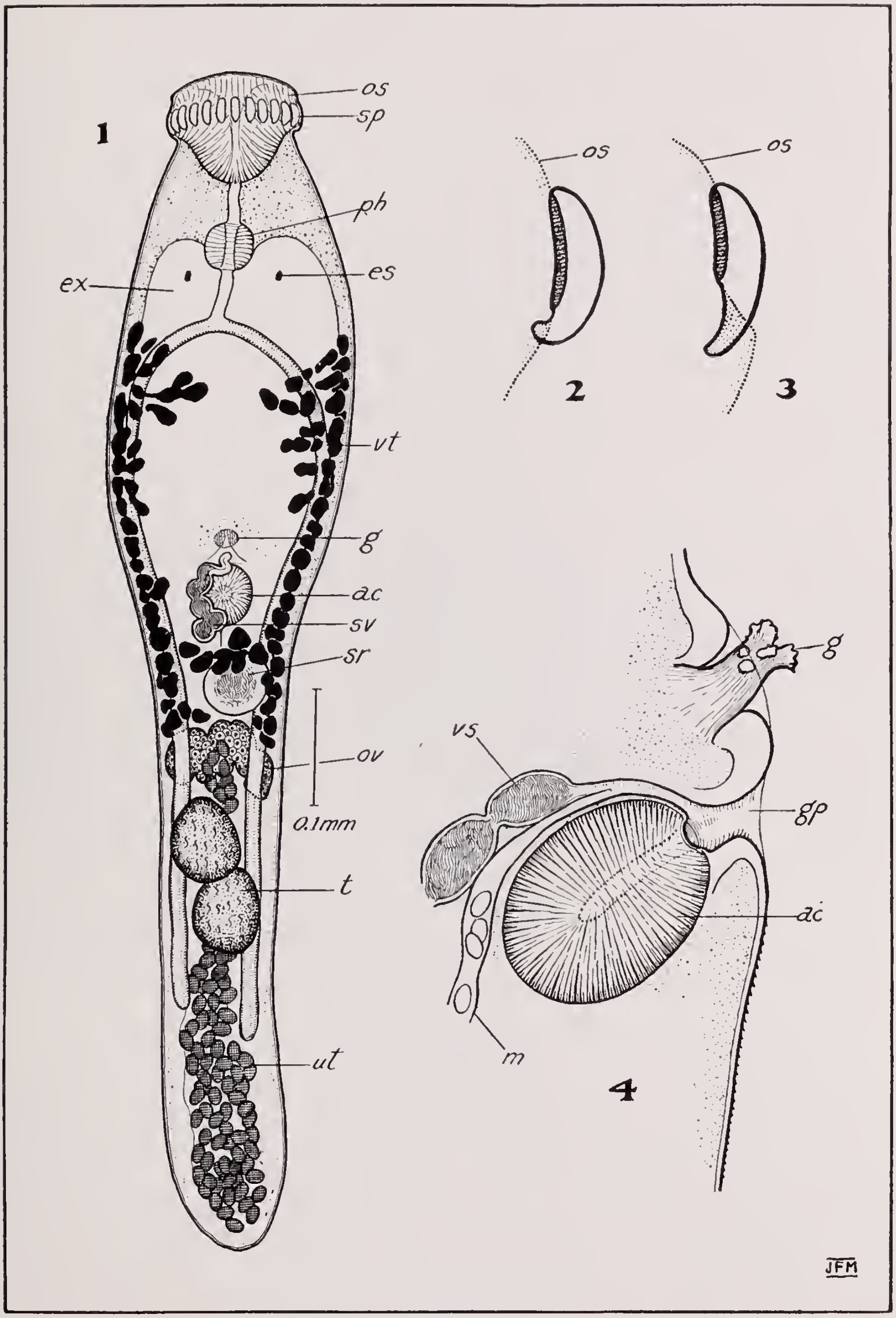
Fig. 3: An oral spine of *A. varius* from same relative position as spine shown in Fig. 2.

Fig. 4: Ventro-genital complex of *A. artus,* seen in side view.

Abbreviations

ac—acetabulum
es—eye spots
ex—excretory bladder
g—gonotyl
gp—genital pore
m—metraterm
os—oral sucker
ov—ovary
ph—pharynx
sp—spines
sr—seminal receptacle
sv—seminal vesicle
t—testis
ut—uterus
vd—vitelline duct
vs—vesicula seminalis
vt—vitellaria

Plate 15



SECTION 1. DESCRIPTIONS OF NEW SPECIES

Trematoda: Family Heterophyidae

The genus Allacanthochasmus has been the subject of diverse opinions as to its family relationship. Poche (1926) ascribed it to the family Acanthostomidae and in this is followed by Fuhrmann (1928). This assignment, as shown in detail in Section 3 of this article, is based upon imperfect understanding of the genitalia. According to the present authors (Van Cleave and Mueller, 1931), the genus Allacanthochasmus belongs to the family Heterophyidae.

As originally defined, the single species included in the genus Allacanthochasmus is so highly variable that *A. varius* was chosen for its specific name. An extended study of living and preserved materials from Oneida Lake fishes has given full confirmation of the presence of an additional species in this genus to which we are attaching the name *Allacanthochasmus artus.*

Allacanthochasmus artus new species

(Figures 1, 2, 4, 55, 56, 63, 67)

Host.—*Lepibema chrysops*, in intestine.

Throughout the program of field studies on the fish parasites of Oneida Lake, both encysted and free immature specimens of the genus Allacanthochasmus have been encountered frequently in a considerable variety of fish hosts. However, we have never found members of this genus reaching full sexual maturity in Oneida Lake in any host other than the white bass (*Lepibema chrysops*). During the first two years of our field and laboratory study we felt relatively certain that all of the specimens in our collections represented the highly variable species *A. varius.* Ultimately, the examination of living worms under high magnification revealed characters readily available for the recognition of two sharply defined groups. These characters are so significant that there can be no doubt of the validity of the new species to which we have assigned the name *Allacanthochasmus artus.*

A review of the approximately two thousand specimens of the genus Allacanthochasmus, which we have stained and mounted for study, from the extensive collections of that genus, reveals the fact that *A. artus* is much less common than *A. varius.* The two forms occur in our collections in the ratio of approximately one *A. artus* to twenty-five *A. varius.*

Reëxamination of the original material serving as the basis for the description of *A. varius,* shows that the holotype of that species and the series of paratypes selected to represent it include no individuals of *A. artus.* However, in the collections from Lake Erie, and from Lake Pokegama in Wisconsin, *A. artus* appears in approximately the same ratio to *A. varius* as that which we have found in Oneida Lake.

Description.—Body elongate, slender, about 1.3 mm. long and from 0.08 mm. to 0.14 mm. in diameter; broadest at the level of the crural fork where the excretory bladder (Fig. 1, *ex*) is greatly dilated. As a consequence of this dilatation of

the excretory bladder, the esophagus and crura hang very free in the body and in unobstructed view, even in whole mounts. Oral sucker funnel-shaped, its lip bearing 26 to 29 prominent cuticular spines arranged in a single circle. Frequently the lip is reflexed to such an extent that the spines diverge from a point posterior to the oral sucker. These spines (Fig. 2) are distinctly different from those of *A. varius* (Fig. 3), in that the posterior tip of each is bent almost at a right angle with the line of attachment, the recurved portion pointing toward the median axis of the worm. Ovary (*ov*) a pretesticular transverse band with fewer lobes than *A. varius.* Vitellaria lateral to crura from ovary anteriorly to near fork of crura; in anterior region the follicles of the two sides become continuous over the dorsal surface of the body. Uterus (*ut*) a single sling in the posterior third of the body, with a descending and an ascending stem winding loosely. Eggs about 0.020 mm. by 0.012 mm., light brown in color. Testes slightly oblique or subserial. Gonotyl (Figs. 4 and 56, *g*) a naked, muscular, stalk-like, cylindrical organ on anterior lip of the ventro-genital sinus, permanently exserted; its apex bears five root-like processes. The largest of these (Fig. 56) is antero-median in position, while a pair of smaller processes occurs on either side in a postero-lateral position. The cuticula adjacent to the gonotyl is thicker than over the general body surface. Seminal receptacle present. Seminal vesicle (*sv*) largely posterior to the acetabulum.

A. artus differs from *A. varius*, its only congeneric relative, in many points, of which the following are among the more significant: (1) form of body (slender in *A. artus,* robust in *A. varius*); (2) form of gonotyl (cylindrical with five root-like processes at apex in *A. artus*, a simple crescentic prominence without lobes in *A. varius*); (3) extent of the uterus (transverse loops filling the posterior third of body in *A. varius* are lacking in *A. artus*); (4) shape of the oral spines (in *A. varius,* Fig. 3, there is no sharp differentiation of root and tip while in *A. artus*, Fig. 2, the tip of each oral spine is sharply set off from the root-like base); (5) development of prepharynx and esophagus (very short or wanting in *A. varius*, fairly well developed in *A. artus*).

In general appearance, *A. artus* bears a close resemblance to *Cryptogonimus chyli* (See Plate 25). The presence of oral spines on *A. artus*, the form of the gonotyl and its relation to the genital sinus are the only significant points of morphological distinction.

Types.—Cotypes of *Allacanthochasmus artus* are deposited in the United States National Museum, and in the collections of the Roosevelt Wild Life Station, Syracuse, New York.

Trematoda: Family Allocreadiidae

The genus Crepidostomum is the most abundantly represented member of this family in the Oneida Lake fauna. The species of Crepidostomum and Megalogonia will be treated in full in our final report. Of the remaining genera in this family, we are here offering descriptions of three new species, one representing the genus Allocreadium (Fig. 5) and two, the genus Triganodistomum (Figs. 6 and 7).

Throughout the course of our field collecting we have thought, on numerous occasions, that the living trematodes before us were members of the genus Allocreadium, but in all of the earlier part of our field study specimens tentatively

Plate 16. New Allocreadiidae.

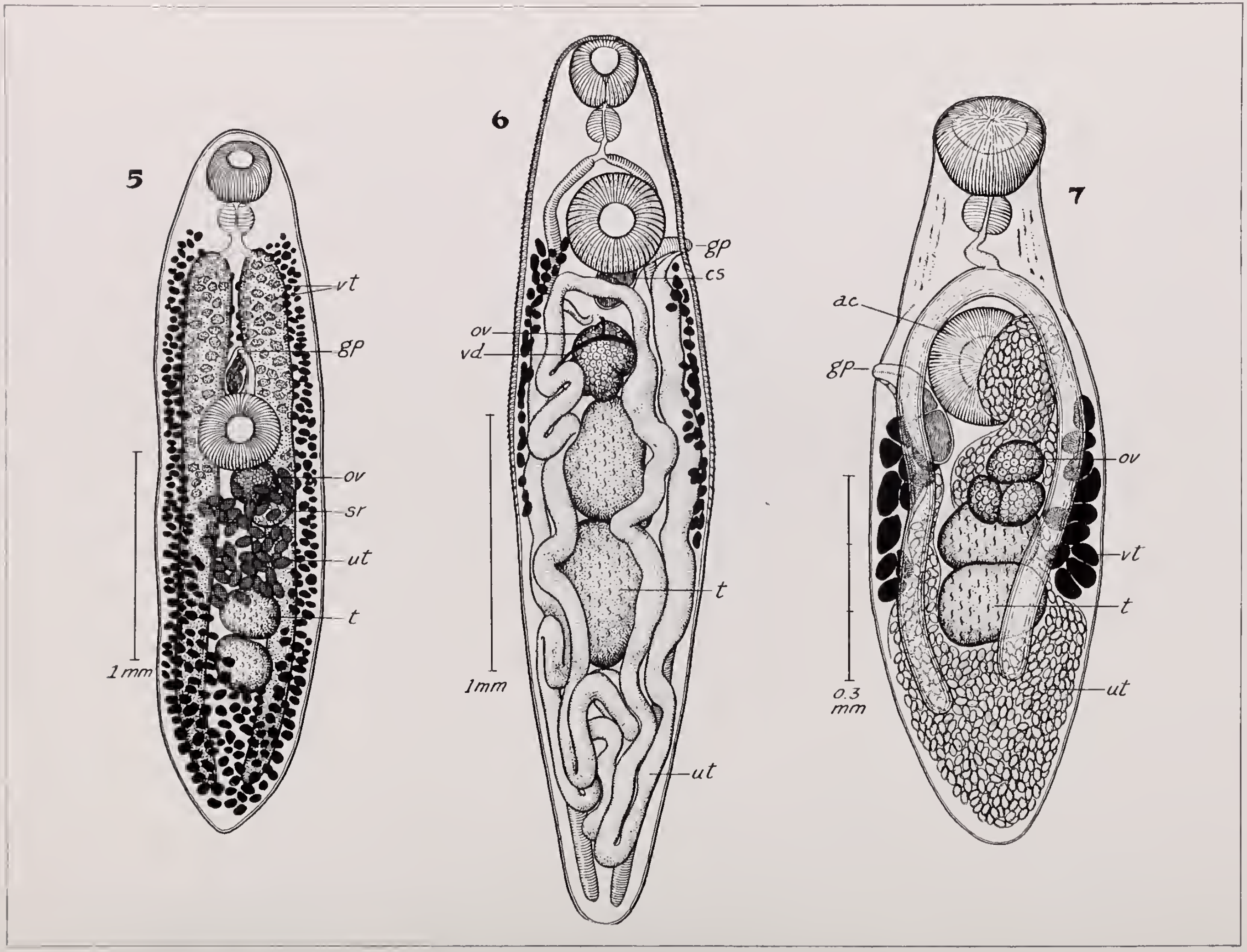
Fig. 5: *Allocreadium halli* new species. Ventral view.

Fig. 6: *Triganodistomum attenuatum* new species. Ventral view.

Fig. 7: *Triganodistomum simeri* new species. Dorsal view.

Abbreviations

ac—acetabulum
cs—cirrus sac
gp—genital pore
ov—ovary
sr—seminal receptacle
t—testes
ut—uterus
vd—vitelline duct
vt—vitellaria


5
vt
gp
ov
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1 mm
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ac
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identified as Allocreadium proved on closer study of stained specimens to belong to other genera. Finally, in the collections of the summer of 1931, two bullheads were found to carry undoubted specimens of Allocreadium, which upon detailed study proved to be a previously undescribed species.

Allocreadium halli new species

(Figure 5)

Host.—*Ameiurus nebulosus,* in alimentary canal.

Two bullheads from the harbor of Cleveland, New York, carried very light infestations with this species. This gives indication that the species is very rare and either has a restricted seasonal distribution or possesses centers of infestation outside the lake with only an occasional host migrant bringing the worms into the lake fauna.

Description.—The sexually mature worms vary in length from 2.5 mm. to 3.5 mm. The body (Fig. 5) is narrow, elongate, with both ends rounded and sides nearly parallel. The oral sucker (0.3 mm.) is nearly spherical and somewhat smaller than the acetabulum (0.4 mm.). The pharynx is about one-half the diameter of the acetabulum, with its length (0.15 mm.) slightly less than its diameter (0.2 mm.). The esophagus is short and quickly branches to form the crura. The crura, which are large and inflated, appear as deeply staining, thick-walled, longitudinal sacs, sharply differentiated in appearance from the esophagus. They reach to the posterior extremity. The genital pore lies on the median line a short distance before the acetabulum. A cirrus sac is present, lapping back over the dorsal surface of the acetabulum. Ovary and testes are rounded, without lobes, the former on the left side at the posterior border of the acetabulum, and the testes contiguous, in tandem fashion, about midway between the ovary and the caudal tip. A receptaculum seminis (Fig. 5, *sr*) is present behind the ovary. The vitellaria extend from the fork of the intestine to the caudal tip, chiefly lateral. Anterior to the acetabulum they arch over the dorsal surface, meeting in the midline, and similarly posterior to the testes they arch over the ventral surface from the two sides, forming a continuous field. The vitellaria are composed of numerous small follicles. The uterus is confined to the space between the anterior testis and the ovary, passing once backward and once forward, and looping several times transversely. The metraterm crosses the dorsal surface of the acetabulum to reach the genital pore.

Pratt (1923:64), in the first survey of the fish parasites of Oneida Lake, reports taking some small trematodes from the bullhead, which should be considered in this connection. He states, "In the intestine of one fish also were obtained many slender Trematodes about one millimeter in length, compressed and mounted, belonging to an undescribed genus allied to *Allocreadium.*" These worms are much smaller than ours, and, if the same form, must have been very young specimens. Unfortunately, this material has been lost and is not available for reëxamination.

Allocreadium halli, which is named after Dr. Maurice C. Hall, more closely resembles *A. ictaluri* Pearse than any other described member of the genus. It

differs from *A. ictaluri* in form of the body, development of the uterus, form of the posterior testis, size of the eggs, and calibre of the intestinal crura.

Types.—The holotype of *Allocreadium halli* is deposited in the United States National Museum. Paratypes are deposited in the collections of the Roosevelt Wild Life Station, Syracuse, New York.

Triganodistomum attenuatum new species

(Figure 6)

Host.—*Catostomus commersonii,* in digestive tract.

Simer (1929) erected the genus Triganodistomum to include a single species which he described under the name *Triganodistomum translucens*. In comparing his new genus with what he deemed closely related forms, he made no comparisons with the genus Lissorchis of Magath (1917), though specimens of that genus were represented in his collections. Simer (1929:571) assigned Triganodistomum to the family Plagiorchiidae. The present writers have been making an extended study of those fish trematodes which bear a lateral genital pore and have arrived at the conclusion that Plagioporus, Plagiocirrus, Triganodistomum, and Lissorchis are all closely related. Despite the fact that these four genera have been assigned to three different families by various authors, we adhere to the view that they represent but a single family and assign them all to the Allocreadiidae. In following this plan we have accepted the proposal of Sinitsin (1931) who, in redefining Plagioporus, placed it in the Allocreadiidae. These four genera, mentioned above, will be discussed in detail in our final report, and characters available for their recognition and separation will be analyzed.

During the summer of 1931, we discovered two new species of Triganodistomum which are clearly distinct from *T. translucens,* to which we are applying the names *T. attenuatum* and *T. simeri*. The description of the first of these follows:

Description.—The type specimen (Fig. 6) of *Triganodistomum attenuatum* is 3.5 mm. in length, and at the widest point about 0.75 mm. in breadth. The suckers are prominent, and the acetabulum (0.4 mm. in diameter) is larger than the oral sucker (0.3 mm.). The acetabulum is located close behind the pharynx, in the anterior fourth of the body. The genital pore is on the left margin, on a level with the middle of the acetabulum. The cirrus sac overlaps the acetabulum dorsally, curving inward and backward, and projecting posteriorly a slight distance beyond the acetabulum. The seminal vesicle is divided into two parts by a transverse partition. The ovary is lobate and median, separated from the acetabulum by a distance roughly equal to its own diameter. The testes, somewhat irregular in outline, are large and lie close together, immediately posterior to the ovary. The space posterior to the testes is almost equal to the space occupied by the testes taken together. The vitellaria are composed of small lateral follicles and extend from the middle of the acetabulum to near the middle of the posterior testis. The transverse yolk duct gives rise to the common duct ventral to and just about opposite the center of the ovary. The uterus passes backward on the left side to the caudal region, loops, passes forward on the right to the level between acetabulum

and ovary, loops again and retraces its course in reverse order, eventually ascending on the left and passing by the ovary and forward to the genital pore. The uterine tube is narrow, well defined, and thrown into loose coils along its course. The eggs are small and numerous, yellow, and have a length of 0.020 mm. and diameter of 0.012 mm. Heavy spines cover the front half of the body.

T. attenuatum is distinctly larger than *T. translucens* and differs from that species in the form of the body, in the relative size of the cirrus and cirrus sac, and in extent of the vitellaria.

Types.—The holotype of *T. attenuatum* is deposited in the United States National Museum. Paratypes are deposited in the collections of the Roosevelt Wild Life Station, Syracuse, New York.

Triganodistomum simeri new species

(Figure 7)

Host.—*Catostomus commersonii,* in digestive tract.

Of the two specimens of the common sucker which serve *T. simeri* as host, one bore a single individual while the other harbored ten worms of this species. The specific name is in honor of Dr. P. H. Simer, author of the genus Triganodistomum.

Description.—Largest specimens are about 1.15 mm. in length. The oral sucker (0.150 mm. in diameter) has a thin lip (Fig. 7) which tends to flare out from the contour of the body, like the sucker of a leech. The acetabulum (0.180 mm. in diameter) is slightly larger than the flared oral sucker and is located well forward in the body. The pharynx (0.082 mm. in diameter) is conspicuously large and is followed by an esophagus. The crura fork anterior to the acetabulum, terminating a short distance posterior to the hind testis. Ovary and testes lie close together in serial order, the trilobed ovary a short distance caudad of the acetabulum. Posterior to the second testis is a length of body roughly equivalent to the length of the three gonads taken together. The vitellaria are composed of relatively few large follicles (from ten to twelve per side) extending laterally from the posterior edge of the acetabulum to the posterior edge of the hind testis. The genital pore is on a level with the center of the acetabulum. The cirrus sac extends a short distance posterior to the acetabulum. A transverse septum divides the vesicula seminalis into anterior and posterior chambers. The uterus is packed with eggs and fills the available space from the posterior edge of the acetabulum to the caudal tip of the body. The eggs, which have a thin, yellow shell, are about 0.024 mm. by 0.012 mm.

The crura of *T. simeri* are much shorter than in *T. translucens* or *T. attenuatum.* The body size of *T. simeri* is similar to that of *T. translucens,* but body form is not so peculiarly modified in the region of the acetabulum.

Types.—The holotype of *Triganodistomum simeri* is deposited in the United States National Museum. Paratypes are in the same collection, and in the collections of the Roosevelt Wild Life Station at Syracuse, New York.

Trematoda: Family Strigeidae

The holostomes or Strigeidae are digenetic trematodes reaching their adult stage in birds and mammals. Many species undergo a portion of their larval development within the bodies of fishes. Since the complete life history is known for but a very few of these larval holostomes, the immature worms are treated as distinct species within groups which have the same status as genera. Several species of holostome larvae have been found in Oneida Lake fishes, one of which has been previously described as new (*Neascus oneidensis*). During the summer of 1931, one additional new species has been discovered, and is here described under the name *Neascus grandis*.

Neascus grandis new species

(Figure 11)

Host.—*Umbra limi.* Cysts in mesenteries.

Four specimens of a previously unknown species of Neascus were taken from cysts in the mesenteries of the mud minnow, collected in a branch of Chittenango Creek, near Bridgeport, New York.

Description.—Body (Fig. 11) consisting of a much elongated, narrow forebody with sides nearly parallel, and a very small hindbody sharply set off from the forebody. Length 1.5 mm., width of forebody 0.360 mm. Hindbody 0.240 mm. long by 0.150 mm. in diameter at point of attachment. Pharynx 0.047 mm. in length, nearly twice the length of oral sucker. Esophagus 0.105 mm. long, equaling length of oral sucker, prepharynx and pharynx combined. Acetabulum small, slightly behind middle of forebody about 0.035 mm. in diameter, widely separated from holdfast organ. Holdfast organ at posterior extremity of forebody large, about 0.170 mm. long by 0.120 mm. across. Holdfast gland indistinct or wanting. Fundaments of the gonads (*r*) large, filling most of the hindbody. Bursa copulatrix and excretory bladder both small.

Neascus grandis differs from all the described members of the group in the shape of the forebody and the relative length of forebody and hindbody. In *N. bulboglossa* and *N. ambloplitis* the hindbody approaches or exceeds the length of the forebody. In *N. vancleavei* and *N. ptychocheilus* the short hindbody is not set off sharply from the forebody as in *N. grandis*. *N. grandis* differs from *N. oneidensis* in shape of the forebody, in location of the acetabulum and in the development of a distinct pharynx in *N. grandis*.

Types.—One microscope slide containing the holotype and two paratypes is deposited in the United States National Museum.

Trematoda: Family Gyrodactylidae

The members of the family Gyrodactylidae are minute trematodes living on the skin and gills of fishes. They undergo direct development, having no intervening free larval stages. Because of their small size, the unsatisfactory status of the nomenclature, and lack of distinctive characterizations of the species in the literature, the North American representatives of this family have been very

Plate 17. New species of parasites from *Umbra limi.*

Fig. 8: Lateral view of *Gyrodactylus cylindriformis* new species, showing character of pharynx and of embryos.

Fig. 9: One of the central hooks from attachment disc of *G. cylindriformis*, in lateral view.

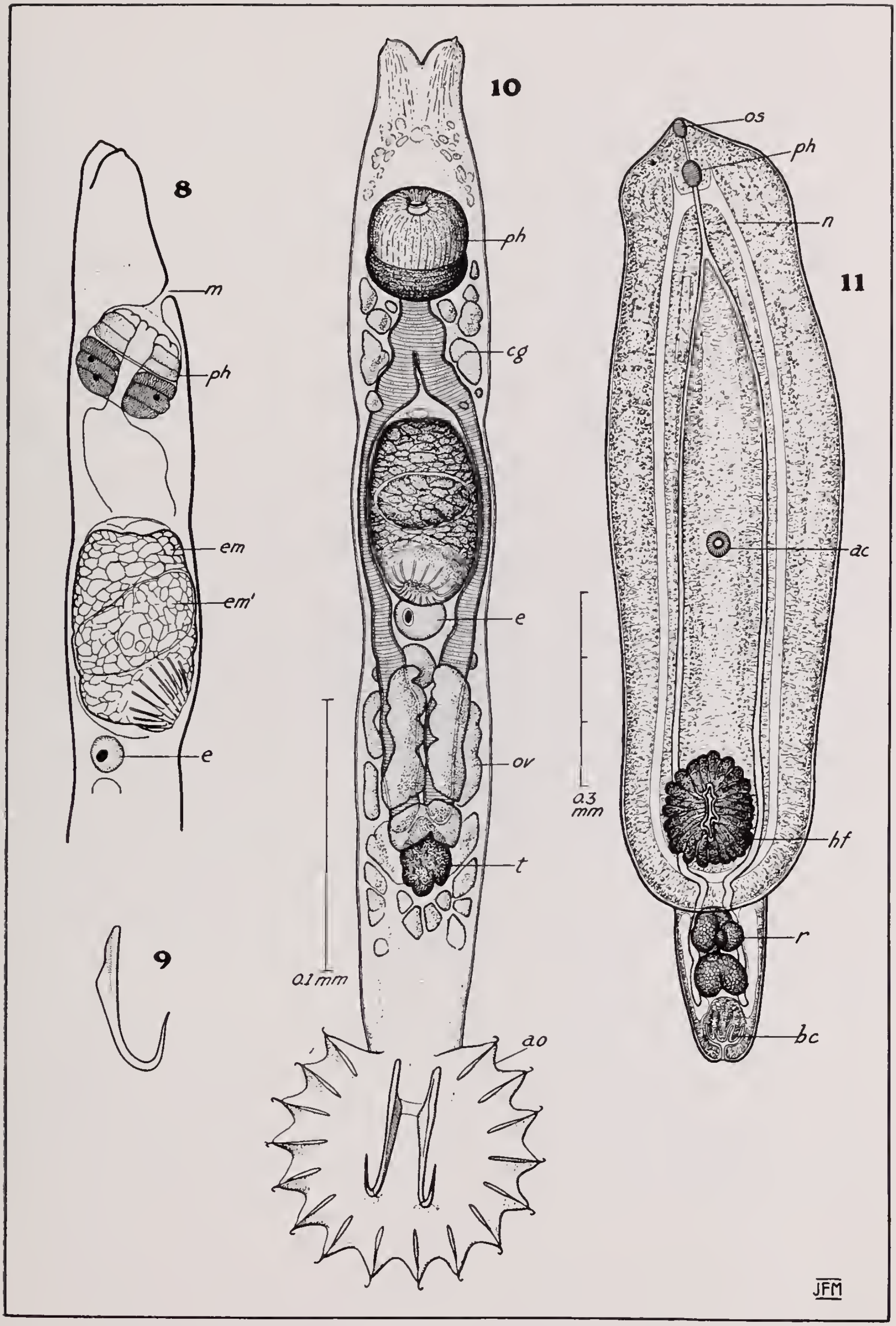
Fig. 10: *Gyrodactylus cylindriformis* in ventral view. Caudal disc in part reconstructed since in all specimens it was embedded in mucus of the host.

Fig. 11: *Neascus grandis* new species. Ventral view.

Abbreviations

ac—acetabulum
ao—attachment organ
bc—bursa copulatrix
cg—cephalic glands
e—egg
em—first embryo
em′—second embryo
hf—holdfast organ
m—mouth
n—nerve
os—oral sucker
ov—ovary
ph—pharynx
r—reproductive organs
t—testis

PLATE 17



imperfectly known. For our fauna, MacCallum (1915) has described a number of species from marine fishes, and Van Cleave (1921) has described a single species of the genus Gyrodactylus from fresh-water fishes. Practically all of the remaining references to the occurrence of members of the family Gyrodactylidae in North America are confined to generic identifications or to problematical determinations under the names of European species. Thus, Hess (1928 and 1930) has recorded the presence of undetermined species of Dactylogyrus and of Gyrodactylus on goldfishes, and an undetermined species of Ancyrocephalus from several species of native fishes in Indiana and central New York. Stafford (1905), Cooper (1915), Ward (1916), Bangham (1926), and Guberlet, Hansen and Kavanagh (1927) have given records of one or more instances of the occurrence of Gyrodactylidae on fresh-water fishes, but have left doubts as to the identity of the species with which they were dealing and in many instances made no attempt at determinations beyond the genus.

In our survey of parasites of Oneida Lake fishes, the minute gill parasites were sought systematically during but one of the summers of field investigation (1931). In this one summer, representatives of all three of the generally recognized genera of the family Gyrodactylidae were found. The rare occurrence of some of the species encountered leads us to believe that members of this family could be studied intensively with great profit. It is certain that they are more abundantly represented in our fauna than the imperfect records would indicate.

Comparison with descriptions of species from other parts of the world indicate that many of our American species are distinct from the better known European and Asian representatives of the same genus. In the forms which have come to our attention, only one species (*Ancyrocephalus monenteron*) is indisputably common to the European and American faunas and this occurs on the gills of Esox on both continents. The carp, which by virtue of its susceptibility to infestation by Gyrodactylidae and because of its dispersal by human agency, might be suspected as an active agent in the dissemination of species, in Oneida Lake bears a fauna wholly distinct from the species present on the same host in European waters. In fact, the great diversity of the species living on the gills of carp, both in Europe and in North America, gives evidence that endemic species of gill parasites in any locality commonly find the carp a susceptible host.

At least under cultural conditions the members of the Gyrodactylidae may assume important economic relations, as revealed especially in the publications of Hess (1928 and 1930) and of Guberlet, Hansen and Kavanagh (1927). For this reason, primarily, it becomes important that the species comprising our American fauna should be recognized and described. Otherwise it is wholly impossible to determine the economic status of any individual species.

Gyrodactylus cylindriformis new species

(Figures 8–10)

Host.—*Umbra limi,* on skin and fins.

We took several specimens of a small Gyrodactylus from the fins and skin of mud minnows collected in a tributary of Chittenango Creek, near Bridgeport, New York.

Description.—Body very small (0.45 mm. long) and very narrow (0.05 mm. wide), chiefly cylindrical but tapering toward the ends. Attachment disc about 0.1 mm. in diameter, its large central hooks having a length of 0.060 mm. from the base of the shaft to the curve. Large hooks have slightly expanded shafts the proximal ends of which are straight, with no inward curve such as occurs in *G. fairporti* and *G. medius.* A thin rudimentary cross piece or clamp connects the right and left hooks about one-third of the distance from their bases. The clamp is simple in outline. No other accessory chitinous structures can be made out. Due to the mucus which adhered to these worms in the preparation, not all of the small hooklets along the margin of the disc can be made out. There are probably sixteen marginal hooklets, since that number is constant for all members of the genus.

Just anterior to the mid-region is the uterus containing a developing embryo. The marginal hooklets of the disc can be seen very clearly in the embryo, grouped in a rosette at one end. A striking feature of this species is the large pharynx, about 0.040 mm. in diameter. In proportion to the size of the worm, this pharynx is far larger than that of other species of Gyrodactylus. The intestine branches immediately posterior to the pharynx, and the two crura pass laterally to the uterus, on either side, and back to about the mid-point between the embryo and the caudal disc. The crura are inflated, with delicate walls. Immediately posterior to the uterine embryo lies the oötype. The ovary extends as a series of lateral lobes from the oötype backward to a short distance from the disc. The median testis lies at the posterior extremity of the ovary, between its terminal follicles.

The head has two lobes, bearing sensory papillae. Eyes are lacking.

G. cylindriformis is very probably specific for the host, *Umbra limi.* This species is the only representative of the genus Gyrodactylus found in our Oneida Lake studies and has never been found on any other host.

There is no former record of the occurrence of Gyrodactylus on the mud minnow. In considering the species with which *G. cylindriformis* should be compared, there have been but three species reported from North America: *G. fairporti* (described by Van Cleave in 1921 from *Ameiurus melas* and *Cyprinus carpio* from culture ponds at Fairport, Iowa); *G. elegans,* and *G. medius.* The last two are common European species reported with some reservations from this continent. From all of these *G. cylindriformis* is readily distinguishable by virtue of its large pharynx.

Types.—The cotypes of *Gyrodactylus cylindriformis* are deposited in the United States National Museum.

Plate 18. *Dactylogyrus extensus* new species.

Fig. 12: *D. extensus* new species, entire worm, in ventral view.

Fig. 13: Detail of egg just within genital pore, and genital hooks seen in side view.

Fig. 14: Side view of tail showing arrangement of hooks and spines.

Fig. 15: Detail study of attachment organ in ventral view.

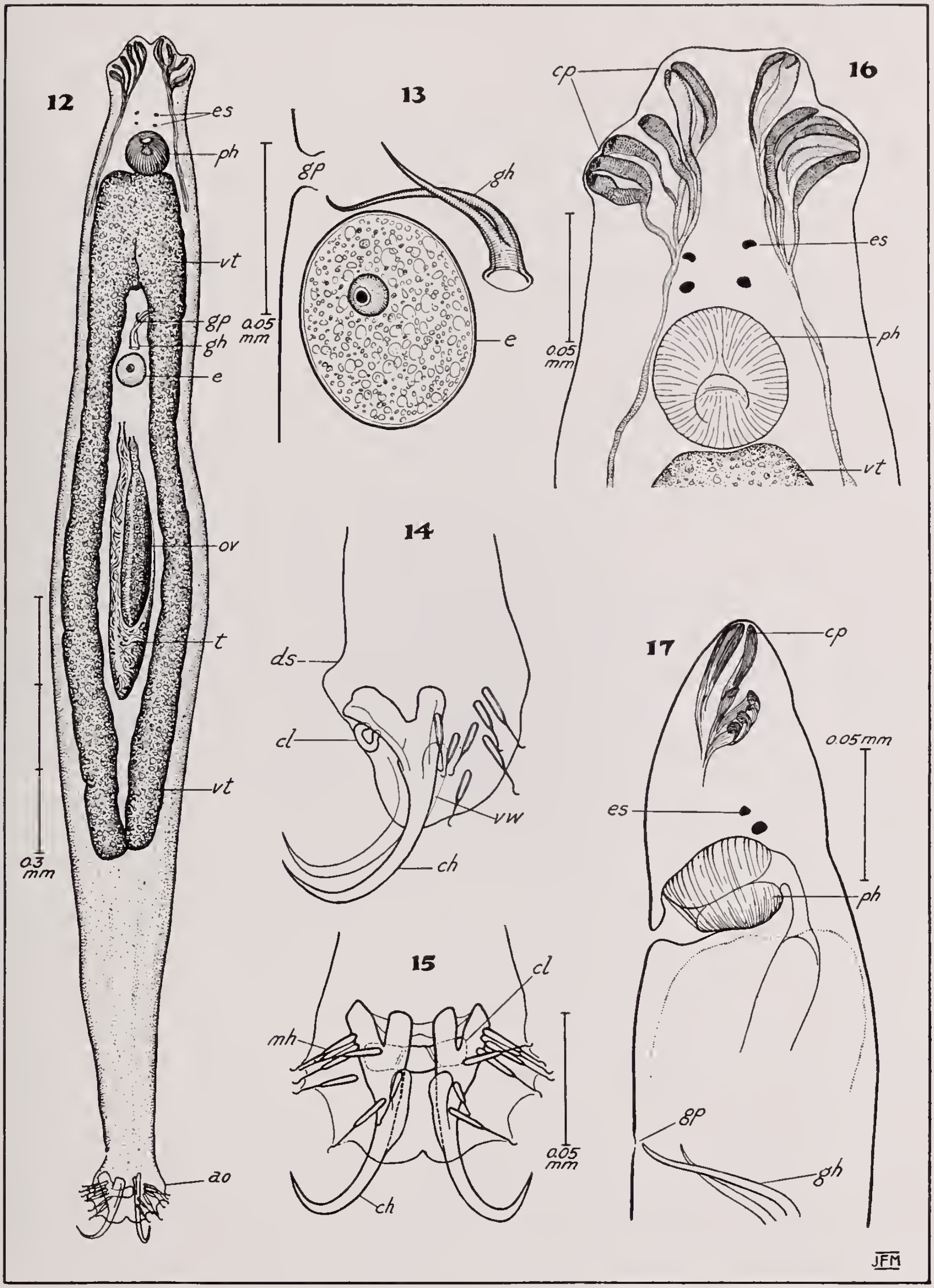
Fig. 16: Detail of head of *D. extensus* in ventral view, showing especially the cephalic papillae and glands.

Fig. 17: Lateral view of head region, showing especially the pharynx.

abbreviations

ao—attachment organ
ch—central hook
cl—clamp
cp—cephalic papillae
ds—dorsal surface
e—egg
es—eye spots
gh—genital hooks
gp—genital pore
mh—marginal hooklets
ov—ovary
ph—pharynx
t—testis
vt—vitellaria
vw—ventral wing of large hook

PLATE 18


12
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ph
vt
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e
ov
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0.3 mm
ao
13
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16
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Dactylogyrus extensus new species

(Figures 12–17)

Host.—*Cyprinus carpio*, on gills.

We examined the gills of a small number of carp for ectoparasites, and in two specimens found Dactylogyrus present. This cannot be recognized as any previously described species and hence is described as *D. extensus* new species.

Description.—Body (Fig.12) very slender, about 1.5 mm. long by 0.1 mm. in diameter. The worms are colorless and die quickly after death of the host. The head bears two pairs of eye spots and irregular marginal lobes which seem to be associated with the cephalic glands. Many of the internal structures cannot be made out in detail in our material, but since these are rarely used in specific descriptions within this genus, attention will be directed to the structures of significant value in classification.

The form of the caudal attachment organ is distinctive of the genus. Two large hooks are present and their free extremities curve dorsally. The attachment organ is only slightly expanded. The marginal hooklets are arranged in two lateral groups, near the posterior corners. The large hooks are sickle-shaped, with a broad base divided into a short ventral process and a longer dorsal process. There is a single clamp (*cl*), dorsal in position, fitting upon the dorsal process of the hooks at about the level of the fork. The clamp is slightly bent and composed of a rolled chitinous plate. The edges of the piece are approximated and turned ventrad. The marginal hooklets have an expanded, tubular base and have a length of about 0.035 mm. Each marginal hooklet at its tip bears a minute sickle-shaped point.

The ovary lies at the middle of the body or slightly anterior, near the ventral surface. The vitellaria commence at the posterior border of the pharynx and extend backward into the posterior region but stop considerably short of the tail. The genital pore is about 0.18 mm. posterior to the pharynx. Just within the pore are two long, slender, chitinous copulatory organs. A single egg is found in the uterus of some specimens, a short distance posterior to the copulatory apparatus.

Hess (1928 and 1930) has reported undetermined species of Dactylogyrus from *Micropterus salmoides*, *M. dolomieu*, *Eupomotis gibbosus*, *Cyprinus carpio*, the goldfish, and other hosts, but has given no description that would serve for identification of his species. Since these references by Hess are the only ones on the occurrence of this genus in North America, any comparisons of *D. extensus* must be drawn between it and species reported from other continents. Lühe (1909) has listed 15 species of Dactylogyrus from Germany alone, and in recent years more than a dozen species have been added to this list for other parts of Europe. *D. extensus* resembles *D. vastator* Nybelin in the lack of a ventral bar connecting the large median hooks of the attachment disc, but the copulatory organs and the large hooks are unlike in these two species. All of the described species differ from the present form in the shape of the central hooks and in their relation to the transverse clamp.

Types.—Cotypes of *Dactylogyrus extensus* are deposited in the United States National Museum, and in the collection of the Roosevelt Wild Life Station, Syracuse, New York.

Cestoda: Family Ptychobothriidae

Cooper (1918) presented an admirable organization of the morphology and taxonomy of the pseudophyllidean cestodes of North America. Within the genus Bothriocephalus, he recognized two species as occurring in fresh-water fishes of this continent. These two were the European species *Bothriocephalus claviceps*, found chiefly in eels, and *B. cuspidatus* which Cooper described as a distinctive North American parasite inhabiting fresh-water fishes, chiefly of the family Percidae. We have found both of these species fairly abundantly represented in our collections of tapeworms from Oneida Lake fishes, and in addition have encountered a third species of Bothriocephalus which differs from all previously described members of this genus. This new species we are describing under the name *Bothriocephalus formosus* in the following paragraphs.

Bothriocephalus formosus new species

(Figures 18 to 21)

Host.—*Percopsis omisco-maycus*, in intestine and ceca.

On several different occasions, we have found this new species of Bothriocephalus in the intestine and ceca of the pirate perch dredged from deep waters of Oneida Lake by means of a beam trawl.

Description.—Small worms rarely exceeding 30 mm. in length, with a maximum breadth of about 1.3 mm. for fixed ripe proglottids. Scolex (Fig. 20) clavate to cylindrical, not sharply set off from neck region, lacking the prominent terminal disc characteristic of most species of this genus. Length of scolex about 0.32 mm. to 0.475 mm.; greatest width about one-fourth the length from the anterior tip, about 0.13 mm. to 0.23 mm. Sucking grooves long, wide, and shallow, very weak and very indistinctly delimited. Scolex almost as thick as wide. Proglottids immediately behind the scolex (Fig. 21) almost the same width as the scolex. Most of the primary proglottids showing one or more transverse divisions but distinct partitions completely separating the secondary products of strobilation frequently lacking even in proglottids bearing mature eggs. Mature proglottids of highly variable form and size in fixed material, in some instances as much as 1.3 mm. wide by 0.2 mm. long, but more commonly from 2 to 3 times broader than long, as, for example, 0.8 mm. to 1.2 mm. in width by 0.4 mm. to 0.6 mm. in length.

Testes about 30 to 45 in each proglottid. Vitelline follicles numerous, occupying almost the whole cortex. Eggs thin-shelled, ellipsoidal, usually about 0.053 mm. to 0.059 mm. by 0.033 mm. to 0.035 mm.

Types.—Cotypes of *Bothriocephalus formosus* are deposited in the United States National Museum, and in the collections of the Roosevelt Wild Life Station at Syracuse, New York.

Plate 19. *Bothriocephalus formosus* new species.

Fig. 18: Proglottid of *B. formosus,* from middle of chain, just before commencement of egg formation. Testes distinct. Ovary somewhat farther forward than usual. Dorsal surface (uterine pore up).

Fig. 19: Proglottid somewhat farther back than the one shown in Fig. 18. Eggs beginning to accumulate in uterus. Testes indistinct. Dorsal surface.

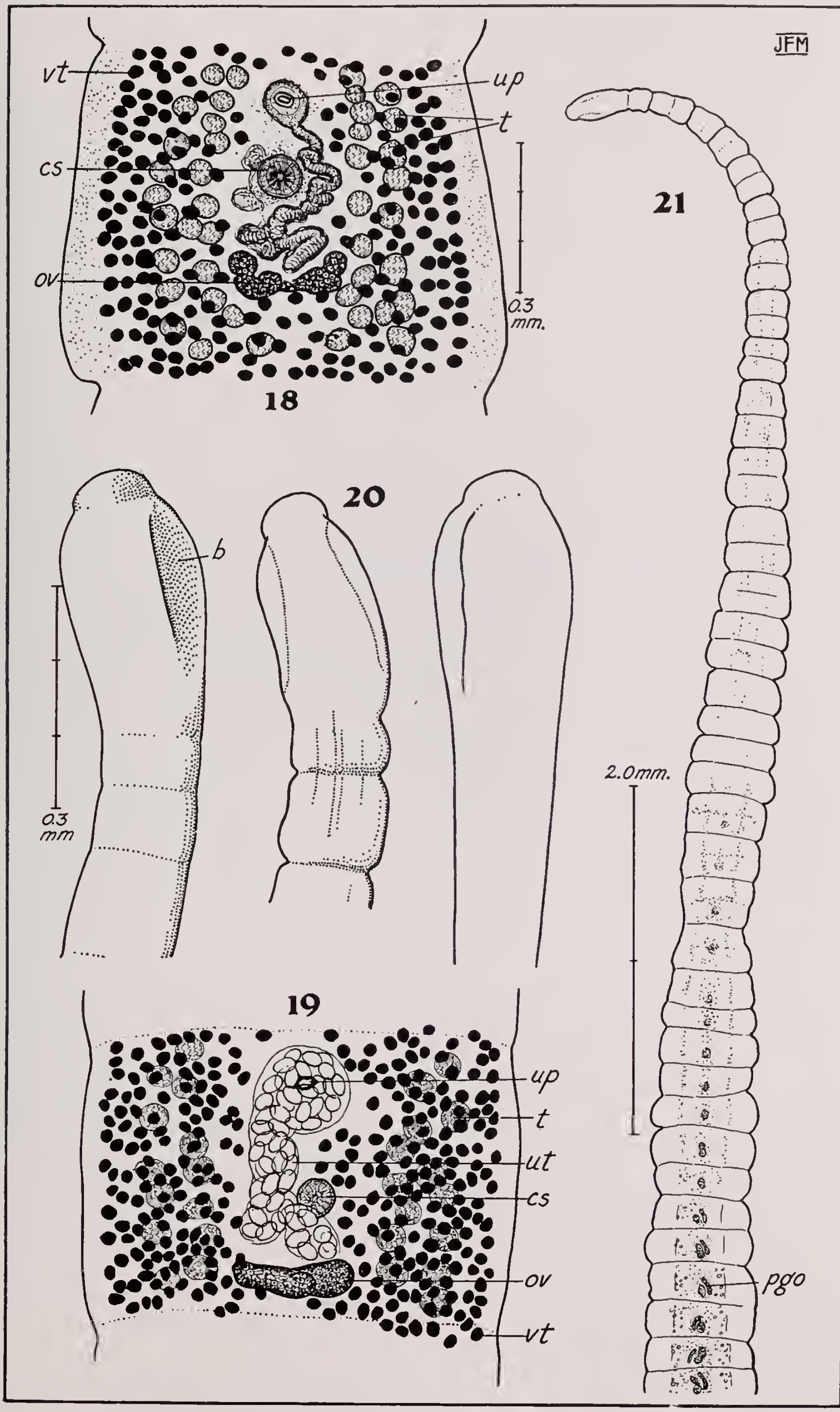
Fig. 20: Three scolices of *B. formosus,* showing shallow bothria and general character of the head.

Fig. 21: Anterior region of a strobila of *B. formosus,* showing form and general appearance anterior to the region of gravid proglottids.

Abbreviations

b—bothria
cs—cirrus sac
ov—ovary
pgo—primordia of reproductive organs
t—testes
up—uterine pore
ut—uterus
vt—vitellaria

PLATE 19



B. formosus may be readily differentiated from those species which have been previously reported from the North American fauna. *B. cuspidatus* is the only exclusively fresh-water species previously described. *B. formosus* has a much smaller strobila and lacks the terminal disc with its prominent notches so characteristic of the scolex of *B. cuspidatus*. *B. claviceps* has been reported once from a fresh-water host other than the eel. We have examined specimens from eels and find them conspicuously different from *B. formosus*. The large size of the strobila and of the scolex and the prominent terminal disc of the scolex in *B. claviceps* serve immediately to differentiate it from *B. formosus*.

B. scorpii, *B. manubriformis* and *B. occidentalis* are all large tapeworms found exclusively in marine fishes. In addition to this difference in habitat, the first two of the foregoing have scoleces much larger than and different in form from the scolex of *B. formosus*. Though the scolex of *B. occidentalis* is not known, the eggs are distinctly larger than those of *B. formosus*.

Nematoda: Family Trichinellidae Ward, 1907

In our collections from Oneida Lake fishes, there are present a considerable number of extremely slender nematodes which, by definition of the Trichinellidae as given by Baylis and Daubney (1926:237), belong within this family and pertain to the subfamily Trichurinae. From this lot of capillariform worms a new species of Capillaria was described in Part I of this report. Additional specimens of a species inadequately represented in our earlier collections were obtained during the field work of 1931. These worms belong close to the genus Capillaria but have morphological characters which compel us to assign them to the genus Hepaticola in spite of a disharmony in host relationship. Since our specimens are distinctly different from the described members of the genus, we are recognizing them as the basis for the description of a new species. This genus is very imperfectly known, and by Yorke and Maplestone (1926:23) is differentiated from the genus Capillaria by a single morphological character. In Capillaria there is a spicule in the copulatory apparatus of the male, while in Hepaticola the spicule is lacking. In the last mentioned genus the copulatory apparatus comprises an eversible membranous sheath, tubular in form but not surrounding a chitinized spicule. In their key to the genera of Capillariinae, Yorke and Maplestone (1926:23) have maintained that occurrence in the liver of rodents (and of man) is a limitation of members of this genus. Inasmuch as the closely related genus Capillaria has a host list embracing the entire vertebrate subphylum, it is not surprising to find Hepaticola in hosts other than mammals. The occurrence in the lumen of the digestive tract of a fish instead of in the liver of a mammal is not readily explained, but in light of the wide host tolerance of many nematodes, it does not seem to warrant the erection of another genus, for in morphological details our new species is in close harmony with Hepaticola. Consequently we are describing this as a new species under the name *Hepaticola bakeri*, in honor of Dr. Hugh P. Baker, Dean of the New York State College of Forestry.

Hepaticola bakeri new species

(Figures 22 to 30)

Hosts.—*Leucichthys artedi tullibee, Notemigonus crysoleucas,* and *Catostomus commersonii,* in the intestine.

Description.—Females 7 mm. to 8 mm. long with a maximum diameter of 0.063 mm. Males 4 mm. to 4.5 mm. in length by 0.045 mm. in greatest width.

In females, the esophagus occupies slightly less than half of the body length, the ratio of the esophageal region to the posterior region being about 2 to 3. The para-esophageal cells of the female begin about 0.13 mm. behind the tip of the head. The anterior esophagus, lying free in the body cavity, is very wide for one of the Trichinellidae. The para-esophageal series numbers about 38 to 40 cells in the females. These cells are cylindrical, elongate, and have transverse superficial grooves (Fig. 29, *div*) giving the appearance of more cells than actually occur. There may be four or more of these constrictions to a single cell. The nuclei are large and vesicular, containing a clear sap and a large, highly refractile nucleolus. The cells are separated by simple transverse partitions. The vulva (Fig. 24, *v*) lies at the posterior end of the para-esophageal series. The eggs (Fig. 26) are thin-shelled, with polar plugs, and have a length of 0.063 mm. and a diameter of 0.033 mm. A mature female contains 20 to 25 shelled eggs in the uterus. The caudal extremity of the female (Fig. 23) is blunt, with the anus on the ventro-terminal angle.

In males, also, the para-esophageal cells begin 0.13 mm. behind the tip of the head. In different worms, we have counted as low as 34 and as high as 38 para-esophageal cells, but the count was made from whole mounts. Since the nuclei can not be seen clearly in all cases we can not be certain of the exact number or if the number is constant. In the largest males, the esophagus equals one-half the body length. The tail (Fig. 30) is blunt, bent slightly ventrad, and the cloacal opening is terminal. Inside the pore, the cloaca has the form of a long chitinous tube or sheath (*sh*), into the forward end of which open the vas deferens and the rectum. This sheath is eversible, and one of our specimens shows the organ in this condition, extending from the caudal extremity as a curving, double-walled, chitinous tube. Evidently as a result of the muscular activity incident to everting the sheath, the tail in this specimen has a reduced diameter for a short distance before its extremity. The extremity itself is clubbed or knob-like (Fig. 25). The reproductive system of the male is a simple tube extending forward from the vas deferens and looping at the posterior end of the esophagus. The testis extends back toward the tail.

This is the first representative of the genus Hepaticola to be reported from the intestine of a fresh-water fish.

Types.—Cotypes of *Hepaticola bakeri* are deposited in the United States National Museum, and in the collections of the Roosevelt Wild Life Station, Syracuse, New York.

Plate 20. *Hepaticola bakeri* new species.

Fig. 22: Anterior extremity of *H. bakeri,* showing length of esophagus lying free in body cavity. The first para-esophageal cell is shown at the bottom of the drawing.

Fig. 23: Tail of female *H. bakeri,* in lateral view.

Fig. 24: Mid-region of female showing vulva and transition from esophagus to intestine. Lateral view.

Fig. 25: Tail of male *H. bakeri,* in lateral view. Sheath everted.

Fig. 26: One egg of *H. bakeri.*

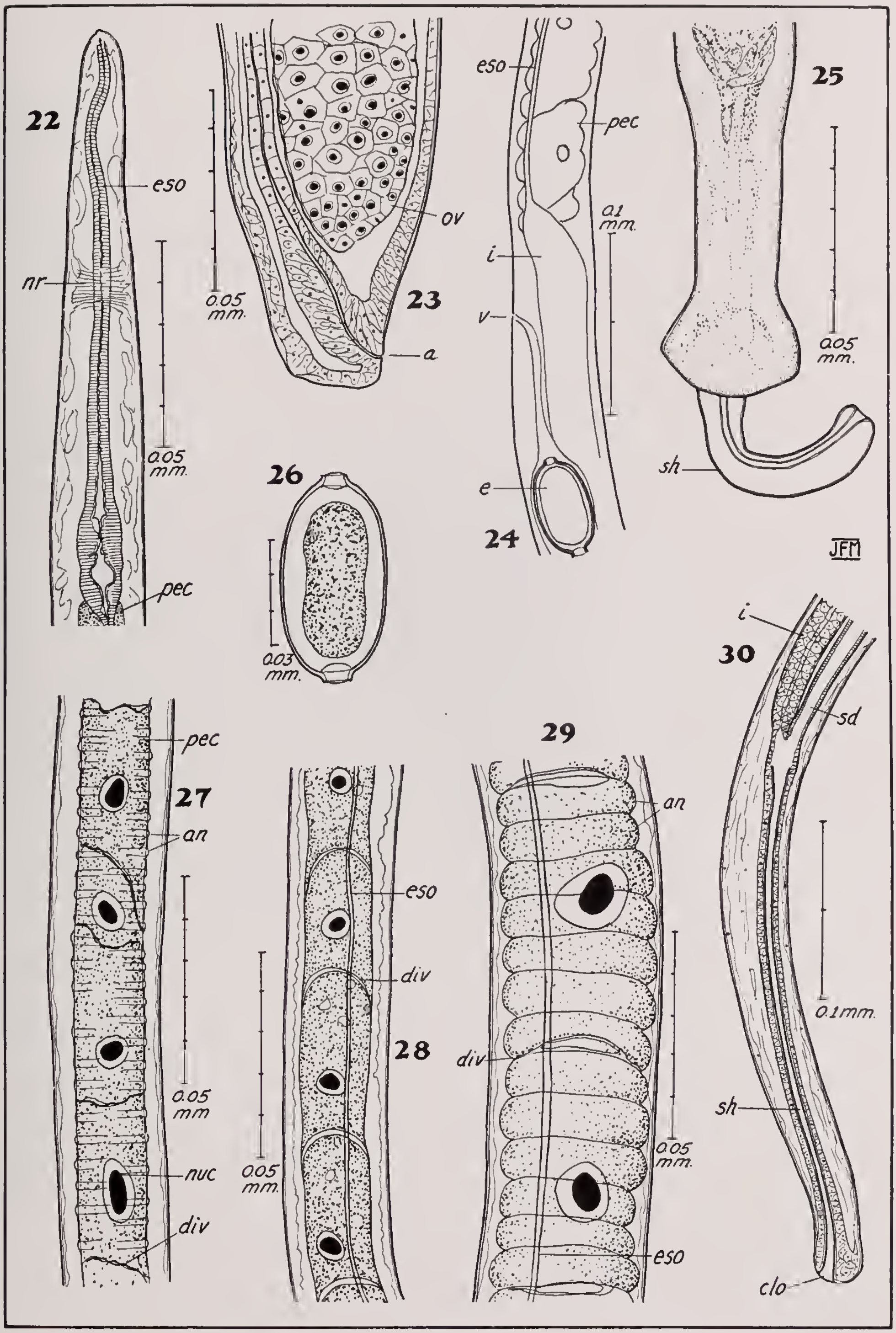
Figs. 27, 28 and 29: Varying appearance of esophageal region of *H. bakeri,* showing para-esophageal cells without annulations, with narrow separate annulations, and with broad contiguous annulations.

Fig. 30: Tail of male of *H. bakeri* with copulatory sheath withdrawn, showing length of sheath, relationships, etc. Note anterior limit of chitinous lining of sheath.

abbreviations

a—anus
an—annulation
clo—cloaca
div—cell boundary
e—egg
eso—esophagus
i—intestine
nr—nerve ring
nuc—nucleus
oj—ovejector
ov—ovary
pec—para-esophageal cell
sd—sperm duct
sh—copulatory sheath
v—vulva

PLATE 20


22
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ov
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24
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25
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26
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JFM
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SECTION 2. REDESCRIPTIONS OF TWO SPECIES OF THE NEMATODE GENUS SPINITECTUS

Specimens belonging to the genus Spinitectus have been the most abundantly represented of any of the nematodes encountered in our collections from Oneida Lake fishes. Recent authorities have differed in the location of this genus. Yorke and Maplestone (1926) have definitely assigned it to the family Rictulariidae while Baylis and Daubney (1926) append Spinitectus to the subfamily Thelaziinae under the Spiruridae. Skinker (1931:374) has referred to the difficulty involved in separating these two families.

Though the specimens of Spinitectus which we have encountered in Oneida Lake fishes during the progress of our field collecting gave evidence of constituting two distinct groups, the tangible basis for separating these became apparent only after the collections had been cleared and subjected to comparative study.

There have been but two species of Spinitectus reported from fresh-water fishes of North America. *S. gracilis* was described by Ward and Magath (1917) and *S. carolini* was described by Holl (1928). The latter is supposedly differentiated from *S. gracilis* on the ground that papillae are present on the tail of *S. carolini*, while Ward and Magath stated that they are lacking on *S. gracilis*.

On the basis of distinctions drawn in the original descriptions of these two species, the present writers were at first convinced that both of the species represented in the Oneida Lake fauna were new, and for a time proceeded on that assumption. One form resembled *S. gracilis* but possessed papillae in the caudal alae while the other resembled *S. carolini* except for the possession of preanal cuticular cleats. After detailed characterizations had been prepared for publication, the essential characters of the two forms checked so closely with those of *S. gracilis* and *S. carolini* that efforts were directed toward a proper evaluation of the points of difference between our specimens and the original descriptions of the two prior species.

Since *S. gracilis* was described from fishes of the Mississippi River at Fairport, Iowa, specimens from that locality in the collections of one of the present writers (Van Cleave) were examined. In unstained mounts, papillae were readily recognizable in the caudal alae of the males but were very much obscured in stained specimens. Professor Ward very kindly placed specimens from the type material of *S. gracilis* at our disposal for reëxamination. Among the stained whole mounts there was a single specimen of a mature male, but the posterior end of this individual was so oriented that observations were made with greatest difficulty. Faint indications of a few papillae could be made out on this specimen but pattern and arrangement of the papillae were wholly unavailable. The simple demonstration of presence of papillae on the type material substantiated by further evidence of papillae on other specimens from the type locality, lead us to conclude that lack of papillae mentioned in the original characterization of *S. gracilis* is not a specific characteristic. Since our specimens from Oneida Lake are especially favorable material for demonstration of the caudal alae and papillae and agree in all other respects with the original description of *S. gracilis*, a rede-

scription of *S. gracilis* is presented in this paper, and the tail of the male (Fig. 36) is illustrated in detail.

The second species which we find in Oneida Lake has many points in common with the distinctive characters of *S. carolini* Holl. After making a careful study of our material, we feel certain that Holl had material of *S. gracilis* as well as of his new species before him when making his description of *S. carolini*. The drawing of the anterior end of a Spinitectus given as figure 1 by Holl is undoubtedly of *S. gracilis,* while Holl's figures 2 and 3 clearly pertain to *S. carolini*. The distinctive short right spicule of the male figured by Holl is in complete agreement with the form of spicule found in our specimens of *S. carolini*. We have never found the muscular esophagus in *S. carolini* extending far anterior to the first body spines though such a condition is regularly present in *S. gracilis*. Furthermore, the pre-anal plates designated as wanting in the description of *S. carolini* are present in our specimens.

In the interest of more complete diagnosis, detailed descriptions of *S. gracilis* and *S. carolini,* based upon our extensive collections, are given below.

Spinitectus gracilis Ward and Magath

(Figures 32, 34 to 36)

Hosts.—*Esox niger, Lota maculosa, Ameiurus nebulosus, Pomoxis sparoides, Esox lucius, Leucichthys artedi tullibee,* and less commonly in *Ambloplites rupestris, Eupomotis gibbosus* and *Salmo fario,* in intestine.

Description.—The mature females from Oneida Lake are 10 mm. to 15 mm. long; males shorter, from 8 mm. to 10 mm. Absolute measurements of size are of little value in describing these forms because of their wide range of variation. The constant features are proportions and anatomical characters, as follows:

The tip of the head (Fig. 32) is conical, without lips. The head cone passes abruptly into the slender, cylindrical neck region. The first row of spines appears just behind the transition from the cone to the cylindrical portion. The body spines are small and numerous. From 17 to 24 spines are usually visible on one side of each ring so that there are from 35 to 50 spines in each circle. The spines are borne on small rounded papillae which emerge from the edge of collar-like cuticular rings. The first few rings (6 to 8) are farther apart (Fig. 32) than the posterior ones. After about the eighth band, the rings are set almost exactly one-half the interval of those anterior. This abrupt change in spacing is not accompanied by any diminution in size of the spines, and the number in a circle remains the same. The rings or spines are not continuous around the circumference of the worm but are divided into dorsal and ventral semicircles. These half-rings, at their point of meeting over the lateral lines, are frequently out of line at the junction so that a slight fault is formed. Sometimes, there is a definite discontinuity marked by an interval without spines. There is a very short oral capsule (Fig. 32, *oc*) and the esophagus in this species begins immediately behind the mouth, far in front of the first ring of spines. The nerve ring lies, usually, between the first and second circles of spines but may be posterior to the third circle. The esophagus is composed of an anterior, slender, muscular region and

Plate 21. *Spinitectus gracilis* and *Spinitectus carolini.*

Fig. 31: Head end of *Spinitectus carolini* Holl.

Fig. 32: Head end of *Spinitectus gracilis* Ward and Magath.

Fig. 33: Vulvar region of *S. carolini* in lateral view, showing short vagina approaching pore from the rear.

Fig. 34: Vulvar region of *S. gracilis,* showing long vagina approaching pore from the front.

Fig. 35: Tail of female of *S. gracilis.* Bluntly tapering.

Fig. 36: Tail of male of *S. gracilis.* Short spicule crooked.

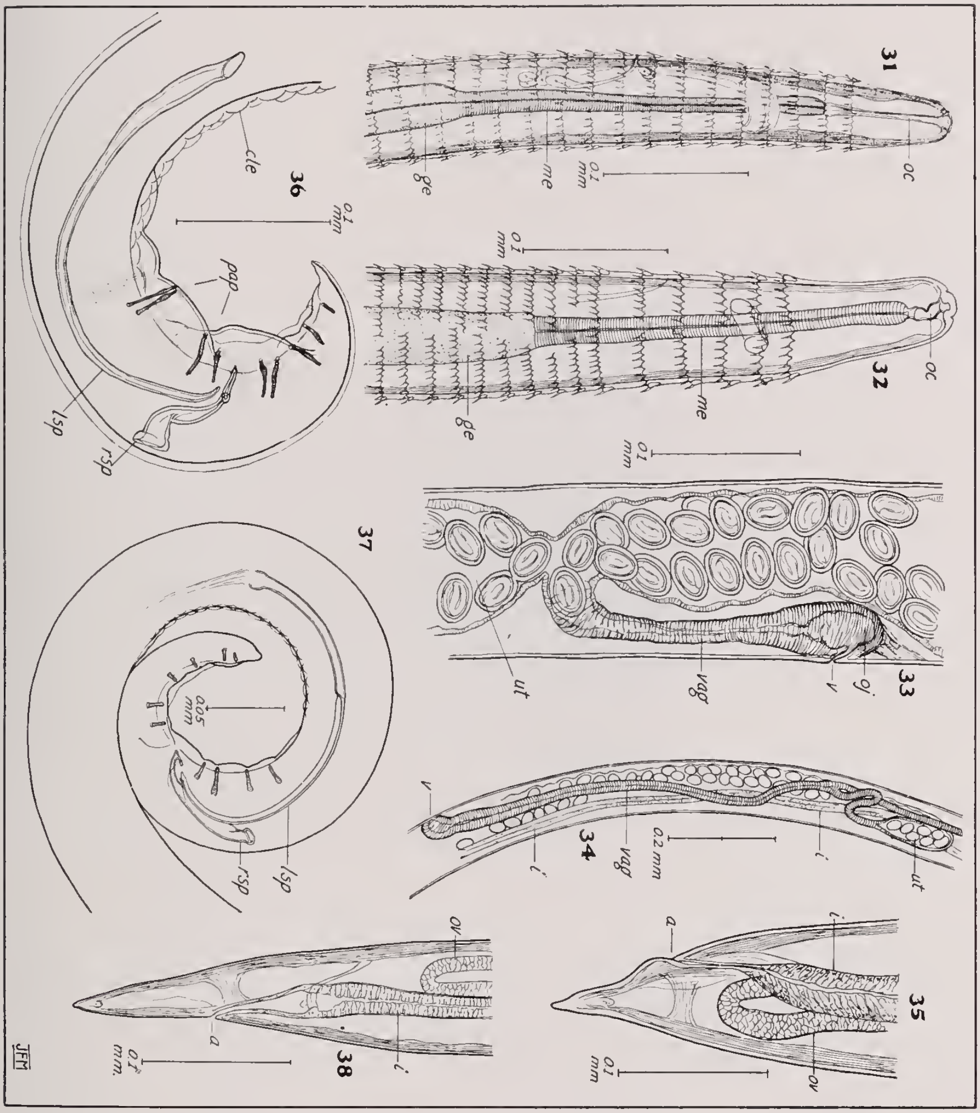
Fig. 37: Tail of male of *S. carolini.* Short spicule arcuate.

Fig. 38: Tail of female of *S. carolini.* Acutely tapering.

abbreviations

a—anus
cle—cleats on cuticula
ge—glandular esophagus
i—intestine
lsp—left spicule
me—muscular esophagus
oc—oral capsule
oj—ovejector
ov—ovary
pap—papillae
rsp—right spicule
ut—uterus
v—vulva
vag—vagina

PLATE 21


31
oc
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JFM

a posterior, thicker, glandular portion. The junction between the two regions occurs at or near the level of the change in interval of the spiny rings. The muscular region of the esophagus equals about one-fourth of the organ. The entire esophagus is, in large specimens, equal to only one-ninth or one-tenth of the body length. In large specimens, there is a tendency for the neck to be drawn out into a long, thread-like portion, followed by the thicker region of the body proper. This differentiation of body regions is not always present, hence cannot be depended upon for specific diagnosis. Likewise, the spines, especially in young individuals, show some divergence from the typical arrangement, and therefore cannot be relied upon as infallibly diagnostic. The vulva (Fig. 34, *v*) lies about one-fourth of the body length from the tail, and the vagina approaches it from the front. A well developed muscular bulb or ovejector is present in this as in other species of Spinitectus. The uterus is bicornuate and branches off from the vagina about 0.8 mm. anteriorly from the vulva, one branch continuing anteriorly, the other turning and passing posteriorly. The tail of the female is abruptly and obtusely pointed and bears the anus very close to its extremity.

The male is similar to the female in the anatomy of the anterior region. The tail is coiled with but a single complete turn in many of the individuals, and has fairly wide alae. Stalked papillae (Fig. 36, *pap*) occur, two pairs pre-anal and three pairs post-anal on either side. Frequently the second papilla of the final pair is lacking or difficult to see. These papillae are borne on slender stalks which are longer than those of the species *S. carolini*.

The left spicule of the male copulatory apparatus is long and gutter-shaped, without any sudden change of form along its length. The right spicule (Fig. 36, *rsp*) is short, thick, and heavily built. It appears to be bent twice, as seen in side view, each time at approximately a right angle. Actually, the spicule is twisted much like a ram's horn. The proximal portion would, by this figure, correspond to the base or mouth of the horn. The tip of the spicule is provided with a large lateral barb. It would seem that this spicule serves chiefly as a gubernaculum for the left, longer spicule. A short distance anterior to the cloacal aperture is a series of cuticular ridges or cleats aligned in longitudinal rows.

The eggs have a diameter of 0.040 mm. by 0.024 mm. They are provided with heavy shells and each bears a coiled embryo at the time of oviposition.

The constant features by which *S. gracilis* may be safely distinguished are: the male spicules; pattern of the male papillae; the position of the anterior tip of the esophagus; ratio of esophagus into the entire worm; size of the eggs and length of the vagina. Other features, not so reliable, are the character of the spination, direction from which the vagina approaches the vulva, and character of the female tail.

Spinitectus carolini Holl

(Figures 31, 33, 37, 38)

Hosts.—*Ambloplites rupestris, Eupomotis gibbosus, Micropterus dolomieu,* in intestine.

Description.—Head cone, as in foregoing species, about 0.08 mm. in length, devoid of spines. The mouth has a smooth edge, without definite lips. The

first circle of body spines occurs about 0.08 mm. from the tip. The spines are very long and sharp, usually fewer in the individual circle than in the preceding species —about twenty-five to thirty-five per ring. Each spine is borne on the edge of a collar-like projection of the cuticula. The edges of these collars are stiffened by a heavy bar of cuticula and bear the papillar elevations on which the spines occur. As in the preceding species, there is usually some discontinuity in the rings over the lateral lines. Successive rings of spines are separated by an interval of about 0.04 mm. and this interval continues posteriorly, increasing somewhat but with a perfectly smooth trend and without any sudden fluctuations in the females, though in the males the internodes between rings become abruptly smaller at about the twentieth ring.

The oral vestibule (Fig. 31, *oc*) is long, and has the structure of a thin-walled, straight-sided cuticular tube. This joins onto the esophagus at the level of the second ring of spines (not at the tip of the head as in the preceding species). The esophagus is divided into an anterior, slender, muscular region and a posterior, thicker, glandular portion. The junction between these lies somewhere between the tenth and the fourteenth rows of spines, the exact position varying in different worms. The ratio of muscular to glandular esophagus is as 1 to 5 or 1 to 6. The entire esophagus equals from one-fifth to one-third the length of the worm. The nerve ring surrounds the muscular esophagus usually between the fourth and fifth rings of spines.

In this species there is never any tendency toward the slender elongation of the neck region frequently observed in *S. gracilis*.

The vulva (Fig. 33, *v*) lies a short distance posterior to the middle of the body. Post-vulvar region of body is to pre-vulvar region as 3: 4. Ovejector well developed, the vagina approaching it from the rear. The bicornuate uterus branches from the vagina about 0.28 mm. posterior to the pore. The eggs are thick-shelled and each bears a coiled embryo upon oviposition. Eggs are 0.036 mm. long by 0.023 mm. in diameter.

The tail of the female (Fig. 38) comes to a long, slender point. It has a very gradual, spear-like taper, as opposed to the blunter, more abrupt termination of *S. gracilis,* and the anus in *S. carolini* is removed a greater distance from the tip.

The male is similar to the female in the anterior body region. The tail (Fig. 37) is usually thrown into a coil of two or three complete turns. Narrow alae are present. The tail is long and slender and the anus farther removed from its tip than in the preceding species. The papillae are provided with short, thick, stalks and tend to be evenly separated rather than paired. The arrangement is four pre-anal and five post-anal papillae on either side of the tail. The right spicule (Fig. 37, *rsp*) is short and arcuate. Its distal end is pointed, while proximally it is expanded. The tip is provided with a large ventral barb. From the large proximal end of the shaft a long curved plate or scute arises and follows along the ventral surface of the spicule, terminating in a point which projects toward the barb. The long left spicule is slender and evenly curved with the general direction of the tail. Its proximal portion is tubular, but about half way along its length it becomes suddenly compressed and rounded into a gutter or trough. The point lies near the barb of the right spicule. Some distance anterior to the anus is a series of par-

Plate 22. The anatomy of *Microphallus ovatus.*

Fig. 39: Detail of cross section of *M. ovatus* in region of genital pore. Edge of acetabulum seen at left.

Fig. 40: Detail of longitudinal section of *M. ovatus,* in region of genital pore. Position of acetabulum and of metraterm dotted in.

Fig. 41: A surface view and frontal sections at three different levels, of the genital complex in *M. ovatus.* A depression of the surface encloses the acetabulum and the genital orifices but is not the equivalent of the ventro-genital complex of the Heterophyidae.

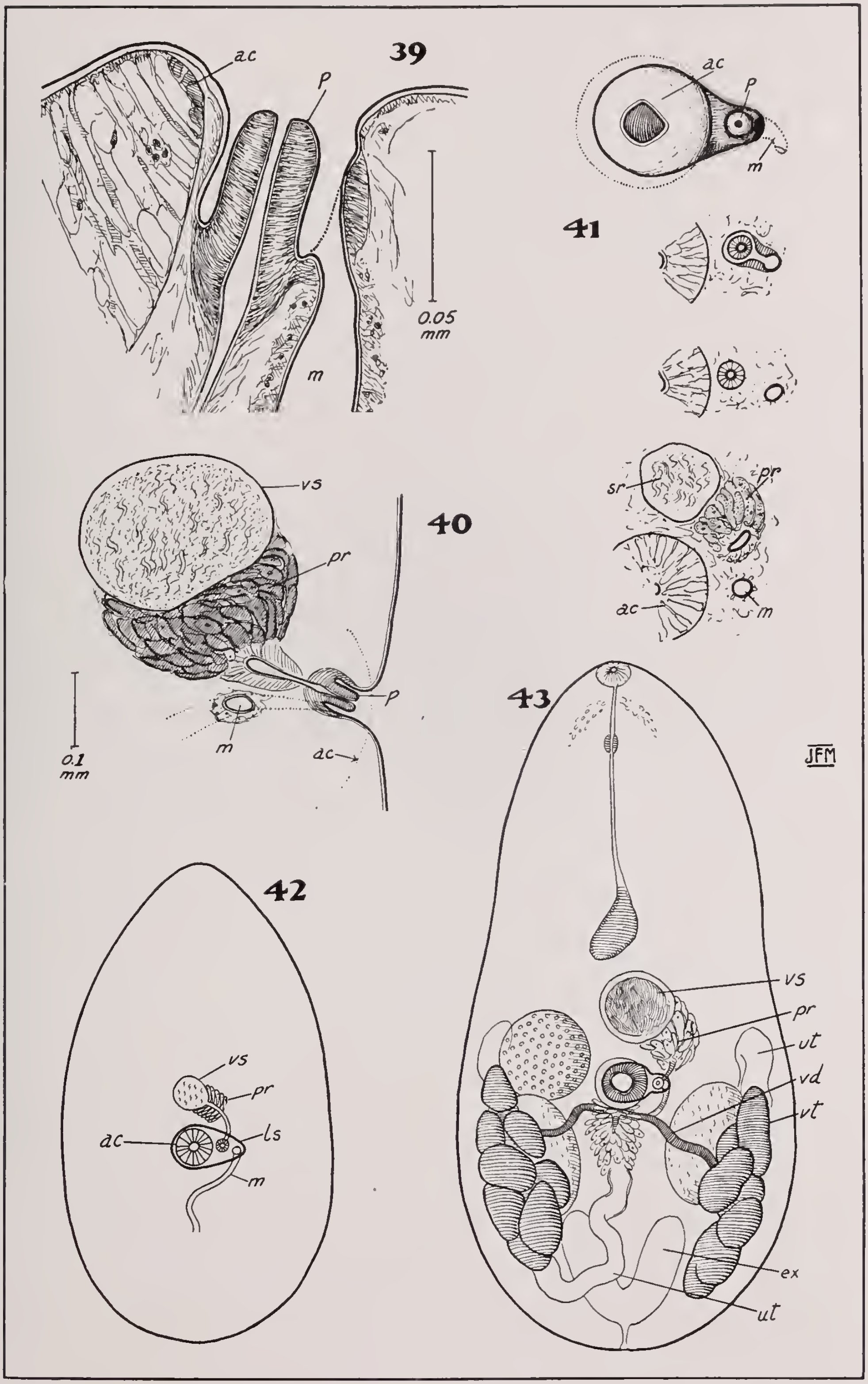
Fig. 42: Diagram of genital complex in Microphallus.

Fig. 43: Ventral view of a toto mount of *M. ovatus.*

abbreviations

ac—acetabulum
ex—excretory bladder
ls—lip of ventro-genital sinus
m—metraterm
p—penis
pr—prostate
sr—seminal receptacle
ut—uterus
vd—vitelline duct
vs—vesicula seminalis
vt—vitellaria

PLATE 22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allel, longitudinal rows of cuticular cleats. These are indistinct in some specimens but are not lacking as stated by Holl.

This worm is smaller than the foregoing species. The mature females are usually from 7 mm. to 8 mm. long at most, and the males are slightly smaller.

S. carolini may be definitely recognized by the following constant characters: shape of the spicules; long oral vestibule with esophagus starting back of the first circle of spines; ratio of esophagus to body length; size of eggs. The following characters are typical but less constant: position of vulva and direction from which the vagina approaches it; the character of the spination; shape of the caudal tip of the female.

SECTION 3. SYNOPSIS OF THE FAMILY HETEROPHYIDAE (TREMATODA) FROM FRESH-WATER FISHES OF NORTH AMERICA

Many of the trematodes reported from fresh-water fishes of North America have been the objects of speculation by various authors who have failed to agree upon their relationships. One of the sources of this confusion has resulted from attempts on the part of some investigators to complete a taxonomic system when available evidences are too meagre to warrant more than a guess at the proper allocation of some of the genera. Many attempts at fitting trematodes from fishes into the general scheme of classification have been made by students interested in details of a portion of a single system, such as the form of the excretory bladder or the topography of the protonephridial system. Important as these individual systems are in reflecting degree of phylogenetic relationship, they give but one line of evidence which must be confirmed by facts from the morphology of other organ systems and from the life cycle. Preconceived notions as to restrictions of certain groups of trematodes to the limits of certain classes of vertebrate hosts have likewise contributed to the failure of some workers to sense relationships of some of the fish distomes.

The writers have studied large numbers of living and preserved collections of trematodes in the course of the survey of fish parasites of Oneida Lake. These investigations have extended over a period of years during which many shifts in tentative conclusions have been necessitated by new lines of evidence. In these studies, an examination of the living worms has frequently offered suggestions as to possible relationship between forms which were originally thought to be entirely distinct. These leads have been followed by the study of whole mounts and serial sections. The fragments of evidence from all available sources, when pieced together, have pointed definitely to a possible solution of many of the disputed questions of supra-generic relationships of the fish trematodes. One of the outstanding results of this study has been the determination of the fact that several genera from fresh-water fishes belong to the family Heterophyidae. Another conclusion is that the genus Microphallus, though very commonly assigned to the Heterophyidae has no direct relation to that family.

Because of their occurrence in mammals and in birds, and their normal or potential infestation of man, the previously known heterophyids have been given considerable attention. In spite of numerous studies on members of this family,

there has been, until recently, a pronounced lack of agreement as to details of morphology in its members and even the confines of the family have been under bitter dispute. Witenberg (1929) has made an especially noteworthy contribution to an understanding of the reproductive organs and the copulatory apparatus in members of this family. His is the most comprehensive systematic treatment of the Heterophyidae that has appeared in the literature. Five subfamilies are recognized in his system, two of which were new in his 1929 monograph. In the same monograph he excluded from the family a number of subfamilies and genera which Poche (1926) and Nicoll (1909) and others had previously ascribed to it. Among these excluded groups are the Microphallinae and the Gymnophallinae, omitted because both lack a seminal receptacle, and in addition, because the former contains reputed members which are provided with a cirrus pouch.

The Heterophyidae have been very generally considered as characteristically reaching the adult state in mammals and birds. In referring to the genus Haplorchis of Looss, Witenberg (1929:200) states: "Two species of the genus Haplorchis are known: *H. cahariuus* (Looss, 1896) and *H. pumilio* (Looss, 1896). It is noteworthy that the first is the only species of Heterophyidae found in the adult state as a parasite of fish. This circumstance leads to the supposition that *H. cahariuus* may belong to quite another family". The present writers have not studied specimens of Haplorchis and find that the descriptions and drawings in the literature are inadequate to serve as a basis for reaching any final conclusions in this matter. However, as shown in the present paper, seven genera of trematodes in the North American fauna regularly occur in fish, yet show characteristics which indubitably unite them with the Heterophyidae (see Van Cleave and Mueller, 1931). Vietosoma, Acetodextra, Allacanthochasmus, Neochasmus, Cryptogonimus, Caecincola and Centrovarium are all normal parasites of fish. In fact, extensive faunal surveys have failed to yield any evidence that members of these genera ever occur normally in either birds or mammals. Consequently there is no possibility that these heterophyid genera are avian or mammalian parasites accidentally misplaced in fishes. The complete agreement of these seven genera with the morphological concept of the Heterophyidae, necessitates the revision of the concept of that family to include the fishes as normal hosts to the heterophyids.

In a footnote, Witenberg (1929:135) calls attention to the fact that the "Heterophyidae are not the only Trematodes with such a complicated genital sinus. Similar structures are also present in other groups of Trematodes, for instance *Microphallus, Hemiuridae, Azygiidae,* etc." After a most thorough investigation of the genital apparatus of Microphallus and of several species of Azygia, the present writers find no difficulty in sharply differentiating between the copulatory modifications and genital sinus of these forms and the ventro-genital complex of the heterophyids. Witenberg's statement regarding the presence of structures similar to those found in the Heterophyidae must be interpreted in the broadest manner, for in the forms which we have investigated there is only the vaguest functional similarity in parts. On the contrary, the genitalia of Vietosoma, Acetodextra, Allacanthochasmus, Neochasmus, Cryptogonimus, Caecincola and Centrovarium are in intimate agreement with the plan of organization generally recognized as distinctive for representatives of the Heterophyidae. In five of these seven enumerated genera, the morphological plan is so similar that a chart has been pre-

Plate 23. Fish trematodes of the family Heterophyidae.

Fig. 44: *Vietosoma parvum,* a heterophyid lacking a gonotyl.

Fig. 45: *Cryptogonimus chyli* in ventral view. A heterophyid with a typical gonotyl.

Fig. 46: *Acetodextra amiuri* in ventral view. A heterophyid with a large gonotyl.

Fig. 47: Detail of ventro-genital sinus of Cryptogonimus, in ventral view.

Fig. 48: Side view of ventro-genital sinus of Cryptogonimus.

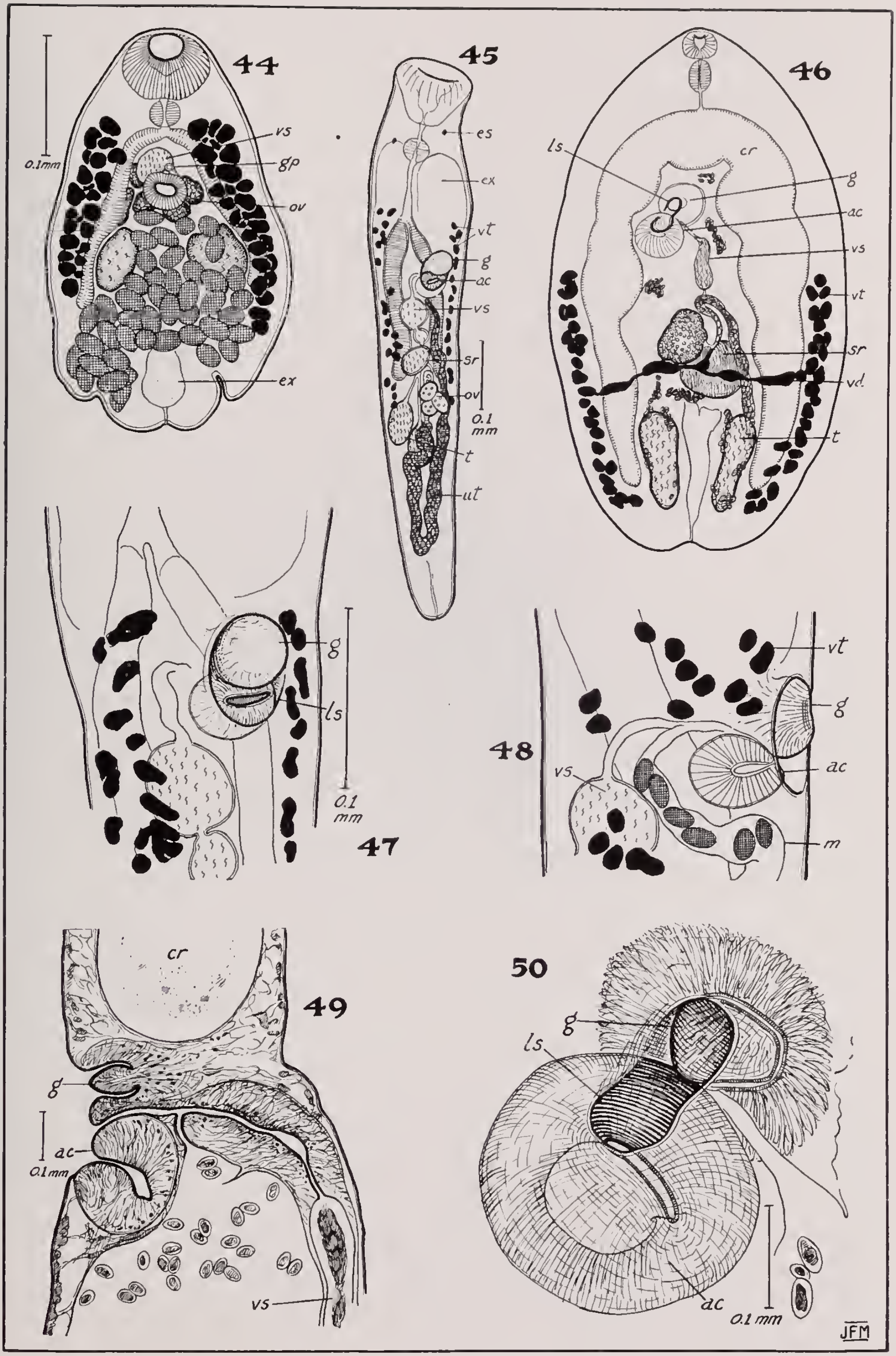
Fig. 49: Detail of ventro-genital sinus of Acetodextra, in sagittal section.

Fig. 50: Detail of ventro-genital sinus of Acetodextra, surface view of a toto mount.

abbreviations

ac—acetabulum
cr—crura
es—eye spots
ex—excretory bladder
g—gonotyl
gp—genital pore
ls—lip of ventro-genital sinus
m—metraterm
ov—ovary
sr—seminal receptacle
t—testis
ut—uterus
vd—vitelline duct
vs—vesicula seminalis
vt—vitellaria

Plate 23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pared (Plate 25) showing the gradual transition of conditions from two stem forms through varying modifications especially of the ovary and of the gonotyl. On the strength of the foregoing evidences, details of which will be set forth in the following section, it seems necessary to modify the definition of the Heterophyidae to include fishes as possible normal hosts of members of this family. Accepting Witenberg's formulation of characters, the definition of the family should be as follows:

Family Diagnosis.—Small to very small trematodes with the body covered with scale-like spines and frequently with a crown of circum-oral spines. Pharynx always present. Body usually divided into a motile anterior, flattened region devoid of genitalia, and a posterior part containing the genital organs. Ventral sucker usually reduced and intimately associated with the genital pore. Genital ducts usually opening into a common genital sinus which frequently contains a copulatory organ known as a gonotyl. Genital pore either median or lateral in position. Ovary and testes highly variable in shape, the ovary almost always anterior to the testes. Cirrus pouch lacking. Seminal receptacle voluminous. Uterus usually not extending anterior to the genital pore. Parasitic in mammals, birds and fishes.

As thus conceived, the family is such a heterogeneous assemblage that limitation by definition of positive characters becomes extremely difficult. Yet, among themselves, the forms here brought together possess a unity of organization that may be sensed by the experienced worker before the detailed points of morphological agreement have been studied out. Thus, the diversity of form and organization here manifested seems to issue as an expression of evolutionary progression (see Plate 25) rather than give evidence of accidental convergence or parallelism. The extent to which evolution has led to diversification is clearly demonstrated by citing a few specific instances of variable conditions in this family. Circum-oral spines may be either present (Fig. 63) or lacking (Fig. 62); either one or two testes may be present; the ovary may be either pre- or post-testicular and in form ranges from spheroidal to follicular; uterine loops may be either wholly pre-testicular or extend to the extremity of the body; and even the ventro-genital sac varies widely in position as well as in the extent of development or of suppression of its component parts. For instance, the gonotyl, one of the most distinctive organs representing a peculiar morphological substitution for the cirrus within many members of this family, may be entirely lacking in some genera (Figs. 65 and 66).

While the gonotyl very commonly occupies a position in the ventro-genital complex anterior to the acetabulum, as in *Heterophyes heterophyes*, its position is highly variable in some other genera. Thus, in Rossicotrema, according to Witenberg (1929:183), there are two small gonotyls at the sides of the genital aperture, while for Dexiogonimus the same authority regards two papillae guarding the anterior and posterior margins of the ventro-genital sac as a peculiarly modified gonotyl. Detailed attention is given to this matter of instability in location of the gonotyl because confusing irregularity has been encountered in the genera considered in this paper. That degrees of relationship within the family Heterophyidae are not clearly shown by conditions of the gonotyl, is shown by the fact that in a single genus (Parascocotyle) two fundamentally different conditions occur. In *P. italica*, according to Witenberg, there is a single, small, oval gonotyl anterior to the ventral

sucker, while in *P. longa* there are two widely separated gonotyls located anterior and lateral to the ventral sucker.

With the understanding that citation of likenesses does not tacitly imply argument for close relationship, the variable conditions in the genera from North American fishes parallel those described for earlier genera by Witenberg. These parallels are as follows: the gonotyl in Neochasmus (Figs. 53 and 69) is posterior to the ventral sucker as in Heterophyes; the gonotyl in Allacanthochasmus, Cryptogonimus, and Acetodextra is anterior to the ventral sucker and the genital pore as in *Parascocotyle italica;* the gonotyl is either completely lacking or has not been recognized in Vietosoma, Caecincola, and Centrovarium, therein paralleling Diorchitrema (Witenberg, 1929:174).

Subfamilies of the Heterophyidae

The family as recognized by Witenberg (1929) includes five subfamilies, but as emended and extended by the present writers (Van Cleave and Mueller, 1932), a sixth subfamily is added to the list, as follows:

1. Heterophyinae Ciurea, 1924
2. Centrocestinae Looss, 1899
3. Haplorchinae Pratt, 1902
4. Cercarioidinae Witenberg, 1929
5. Adleriellinae Witenberg, 1930
6. Neochasminae Van Cleave and Mueller, 1932

Adhering to the view that the Heterophyidae, as an entire family, are restricted to avian and mammalian hosts, Witenberg (1929) has made no direct reference to host limitations in diagnosis of the subfamilies. The fact that five of the genera from North American fishes fit readily and naturally into the Heterophyinae by the simple extension of the host list to include fishes as possible adult hosts, leads us to propose an emendation of the subfamily Heterophyinae. By extending the bounds of this subfamily, we avoid the necessity of creating a new subfamily for Acetodextra and another for Vietosoma. Likewise the Cryptogoniminae of Osborn (1903), though never previously assigned as a subfamily under the Heterophyidae, is based upon a concept which falls wholly within the Heterophyinae except for the fact that its members are from fishes. If thus emended, the subfamily Heterophyinae would include the following genera characteristically found in fresh-water fishes of North America: Vietosoma, Acetodextra, Cryptogonimus, Caecincola, and Centrovarium. The genera Neochasmus and Allacanthochasmus cannot be accommodated in this or any other generally recognized subfamily. It was for this reason that the present writers (Van Cleave and Mueller, 1932) established the subfamily Neochasminae for the former of these genera. Recent studies presented in this paper for the first time have yielded results which permit the inclusion of Allacanthochasmus in the subfamily Neochasminae.

It has seemed to the writers that the diagnosis of the subfamily Heterophyinae is lacking in enumeration of positive characteristics. However, for the purposes of the present synopsis, the delineation of Witenberg is accepted with the simple

extension to include fishes as normal hosts of this subfamily. With this slight emendation, Witenberg's characterization is as follows:

Subfamily Heterophyinae Ciurea, 1924

Diagnosis.—Body more or less flattened, more so anteriorly than posteriorly; no dilation of the anterior extremity; no circum-oral spines; two testes situated behind the other reproductive organs. Reaching the adult stage in mammals, birds and fishes.

In the following paragraphs the genera newly ascribed to the Heterophyinae will be discussed and the morphological evidences supporting the assignment to this subfamily will be set forth individually for each genus.

Heterophyinae: Genus Vietosoma Van Cleave and Mueller, 1932

(Figure 44)

The genus Vietosoma, described in Part I of this report, shows such marked resemblance to the genus Euryhelmis (= *Distoma squamula*) that parallelism does not seem as readily available for explaining the likenesses of the two forms as does an assumption of phylogenetic relationship. The striking similarity between Euryhelmis and Vietosoma was set forth in the original description of the latter (Van Cleave and Mueller, 1932:16). At that time structures which were interpreted as a cirrus and cirrus sac were described for Vietosoma, but in rechecking our material we have discovered that these structures were misinterpreted and that in plan of organization the ventro-genital sac of Vietosoma is distinctly heterophyid. The intimate agreement of Vietosoma and Euryhelmis can find expression only by assigning the two genera to the same subfamily.

At the time when he prepared his monograph on the Heterophyidae, Witenberg (1929) declared that the morphology of Euryhelmis was too little known to permit of its admission to the Heterophyidae. This exclusion was contrary to the expressed opinion of Poche (1926:150), who, in replacing the preoccupied name Eurysoma with the valid designation Euryhelmis, assigned the genus to the heterophyid family. It remained for Baer (1931) to make a detailed morphological study of Euryhelmis, thereby providing the conclusive evidence of its family relationship. The demonstration of a clearly defined ventro-genital sinus, bearing a perfectly characteristic gonotyl, removed the last vestige of doubt concerning the assignment of Euryhelmis to the Heterophyidae. Since Euryhelmis is accorded an unimpeachable status within the subfamily Heterophyinae on the basis of Baer's morphological study, and was assigned to that subfamily by that author as well as by previous workers, we have no hesitation in proposing to place Vietosoma in the Heterophyinae.

In details of organization of the ventro-genital apparatus, the genus Vietosoma offers some perplexing problems. A study of whole mounts gives evidence of a differentiated ovoidal mass lying anterior to the ventral sucker. In surface view this mass is strikingly similar to a gonotyl. In fact, the surface view of the ventro-genital complex is almost identical with that figured by Baer (1931, Fig. 17b) for Euryhelmis. However, in serial sections of Vietosoma we have been unable to

demonstrate the presence of any structure that might be called a gonotyl. The minute size of the worm makes interpretation of details of morphology extremely difficult. In serial sections, the genital ducts of both sexes are clearly demonstrable, for both open in truly heterophyid manner by a common aperture at the anterior border of the ventral sucker. This condition does not form a basis for excluding Vietosoma from the Heterophyinae, for, as shown in an earlier paragraph, the gonotyl may be either present or wanting in the heterophyids.

Heterophyinae: Genus Acetodextra Pearse, 1924

(Figures 46, 49, 50)

In 1900, J. Stafford described a trematode from the liver and the air bladder of a catfish, under the name of *Monostomum amiuri.* He expressed the belief that the name by which he had "chosen to designate it, can not, as far as I at present see, prove either vague or conflicting." In 1924, A. S. Pearse erected the genus Acetodextra to contain as type Stafford's reputed monostome. The original definition of Acetodextra definitely calls attention to the presence of a dextral acetabulum, and while the genus was removed from the monostomes to the distomes, Pearse made no further attempt to allocate it with reference to family or subfamily groups. No subsequent author has offered evidence of the systematic position of Acetodextra, until the present writers (Van Cleave and Mueller, 1931), in a preliminary abstract, proposed placing this genus in the family Heterophyidae. By emending the diagnosis of the Heterophyinae to include fishes as natural hosts of this subfamily, the genus Acetodextra may be accommodated in this subfamily.

A preliminary study of stained whole mounts (Fig. 46) of *Acetodextra amiuri* (Stafford), from the swim bladder of *Ameiurus nebulosus* and *Ameiurus natalis* from Oneida Lake, gave evidence of intimate association (Figs. 49 and 50) of the acetabulum and another sucker-like organ originally interpreted as the genital pore. In Stafford's drawing accompanying the original definition of *Acetodextra amiuri* (1900, Fig. 2) the acetabulum is plainly figured, as Pearse (1924:147) has previously stated, and in addition, a second sucker-like organ is represented adjacent to the anterio-mesial margin of the acetabulum. This last mentioned structure is evidently what the present writers were at first inclined to consider as a highly modified genital pore, and Pearse (1924:147 and Fig. 6) seems to have made the same interpretation.

Later, a study of whole mounts under high magnification and with more favorable illumination, revealed the fact that a groove-like depression (Fig. 50) connects the acetabulum and the second sucker-like organ and that the genital pore lies within this groove at the margin of the acetabulum The details of the relationship between genital pore, acetabulum and the sucker-like body were studied out in serial sections (Fig. 49). In all essential details, these parts are in complete agreement with the ventro-genital complex which Witenberg (1929) has described for members of the family Heterophyidae. The acetabulum is not located on the surface of the body but is so deeply submerged that in cross sections of the worm, in some instances, it is about equidistant from dorsal and ventral surfaces. In frontal sections, a lenticular body, similar in shape to that described by early workers on the Hetero-

Plate 24. Fish trematodes of the family Heterophyidae.

Fig. 51: *Neochasmus umbellus* in ventral view.

Fig. 52: Detail of genital complex of *N. umbellus,* in surface view.

Fig. 53: Detail of genital complex of *N. umbellus,* in side view.

Fig. 54: Detail of poral region of *N. umbellus.*

Fig. 55: *Allacanthochasmus artus,* for comparison with Fig. 57.

Fig. 56: Detail of genital pore complex in *A. artus.* At the left, are shown the tip of the gonotyl (above) and a cross section through the base of its stalk (below).

Fig. 57: Ventral view of toto mount of *Allacanthochasmus varius* for comparison with *A. artus* shown in Fig. 55.

Fig. 58: Cross section through *A. varius* in region of gonotyl (g), showing also cross section of the common genital duct (d).

Fig. 59: Cross section through acetabular region of *A. varius.*

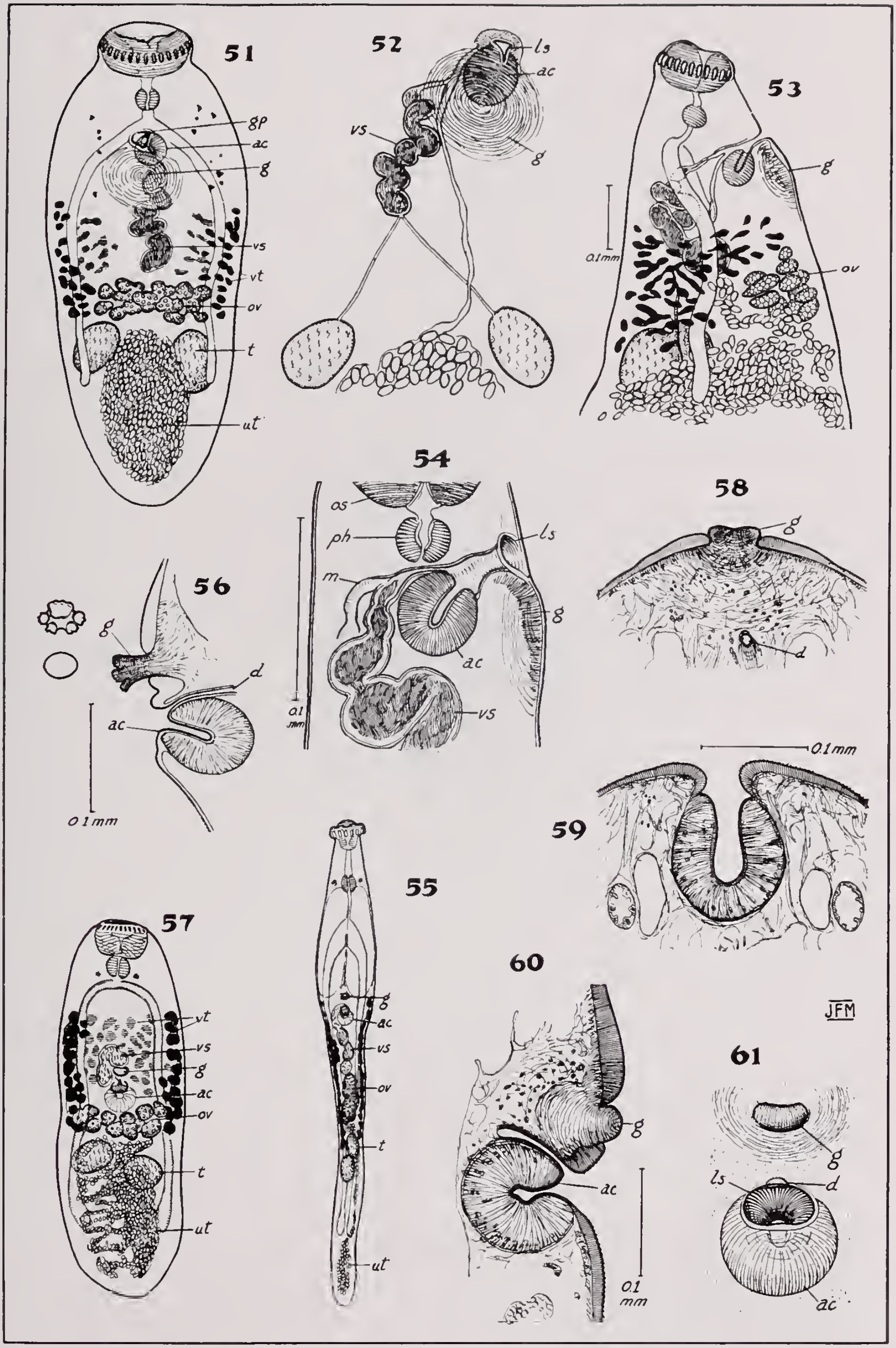
Fig. 60: Sagittal section through genital complex of *A. varius,* showing gonotyl, genital duct and acetabulum.

Fig. 61: *A. varius,* surface view of ventro-genital complex, from a toto mount.

abbreviations

ac—acetabulum
d—genital duct
g—gonotyl
gp—genital pore
ls—lip of ventro-genital sinus
m—metraterm
os—oral sucker
ov—ovary
ph—pharynx
t—testis
ut—uterus
vs—vesicula seminalis
vt—vitellaria

Plate 24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phyidae, is readily distinguishable within the second sucker-like body of the ventral surface. This body is clearly the direct equivalent of the modified male copulatory organ or gonotyl as described and named by Witenberg (1929:235). In sagittal sections the gonotyl (Fig. 49, *g*) is cut in a plane approximately transverse to its long axis, hence in a single section it has the appearance of a small copulatory papilla such as has been described by several authors for Microphallus and other genera. However, the gonotyl of Acetodextra does not surround the terminal portion of the ductus ejaculatorius as in Microphallus. Instead, both genital ducts open into a common atrium (Fig. 49) which communicates with the surface by a single genital pore lying between the acetabulum and the gonotyl. There is no direct continuation of the male duct and the gonotyl.

To the present time we have been unable to find specimens of Acetodextra with the gonotyl exserted. In many of our specimens, the gonotyl is so tightly drawn back into the genital sinus that it is distinctly flattened and gives no clue to its form during copulation. The gonotyl is especially difficult to demonstrate in large specimens. This fact seems to be correlated with the observation that mature worms of this species store the eggs within the body and that the body finally undergoes senescence and disintegration in the swim bladder of the host. It is entirely possible that the initiation of degenerative changes leads to the absorption and final disappearance of some organs, including the gonotyl, before the complete dissolution of the body.

General topography of the other organ systems, as well as the details of the ventro-genital complex, gives additional evidence of the heterophyid relationships of Acetodextra and warrants its being ascribed to the subfamily Heterophyinae.

Heterophyinae: Genus Cryptogonimus Osborn, 1903

(Figures 45, 47, 48, 62, and 64)

The genus Cryptogonimus was originally described as having two ventral suckers. All subsequent authors, except Fuhrmann (1928:118), have quoted Osborn (1903:316) and have idealized one of his original figures but have failed to give consideration to his drawing of a sagittal section. Otherwise, an interpretation of this second ventral sucker would have been made earlier. In this figure, as well as in his description, Osborn shows that "These suckers are contained within a sheath formed as a depression of the ventral surface, and having a lip furnished with a circular sphincter muscle capable of closing the lip to a considerable extent and thus enclosing the suckers. The genital opening is located in the middle line between these suckers, it is thus entirely within the sheath, whence the generic name assigned." The acetabulum and its associated organs thus described form a perfect picture of the ventro-genital complex of the Heterophyidae.

Poche (1926:165) placed the genus Cryptogonimus in the family Acanthostomidae. In this he followed Odhner (1911:522), but at that early date the nature of the ventro-genital apparatus of the Heterophyidae was very imperfectly understood, and the significance of the ventro-genital complex in taxonomy of the trematodes was not at all appreciated. Fuhrmann (1928:118) sensed the fitness of including Cryptogonimus in the Heterophyidae even though details of the genital complex were probably unknown to him. According to his scheme, Cryptogonimus

was placed in the subfamily Heterophyinae where we are content to allow it to remain. Old evidence construed in the light of new interpretations renders Poche's assignment to the Acanthostomidae untenable and gives validity to Fuhrmann's decision.

In sagittal sections, the "double ventral sucker" of the original description, quoted so generally by subsequent writers, proves to be a portion of the ventrogenital complex within a depressed area (Figs. 47 and 48) consisting of a submerged acetabulum and a gonotyl with the genital pore between them. The gonotyl of Cryptogonimus may be cupped, like an acetabulum, but more commonly the end is flattened. The gonotyl (Figs. 47 and 48, *g*) almost fills the ventrogenital sinus and its large, blunt end either protrudes slightly from the orifice or is almost flush with the body surface.

In all essential details, specimens of *Cryptogonimus chyli* agree with Witenberg's diagnosis of the family Heterophyidae and with the typical subfamily as emended in this paper. In the original characterization of the genus, Osborn definitely stated that a seminal receptacle is lacking. This in itself would tend to throw doubt upon heterophyid affinities for Cryptogonimus. However, we have been able to demonstrate a seminal receptacle (Fig. 45, *sr*) in our specimens. This organ lies anterior to the ovary and to the left. In some specimens this is difficult to demonstrate because of the readiness with which it may be confused with the seminal vesicle (Fig. 45, *vs*).

The extent of the uterus was at one time deemed a limiting character marking membership in the Heterophyidae. More recent workers have not agreed with Ransom (1920:528) in specifying that the heterophyid uterus must be pre-testicular. Thus, for example, though the genus Parascocotyle is unquestionably heterophyid, its members show great diversity in uterine extent. In *P. longa* the uterine loops are wholly pre-testicular, while in *P. italica* they occupy the entire area behind the genital orifice, extending post-testicularly to the extreme end of the body. Similar contrasts are found in the different species of the genus Ascocotyle of which Travassos (1930) considers Parascocotyle a synonym. No character so inconsistent within a genus can be entrusted with significant value in determining family limits. Hence, the present writers are in accord with Witenberg in his omission of reference to the extent of the uterus in diagnosing the family Heterophyidae.

In ascribing the genus Cryptogonimus to the subfamily Heterophyinae, attention should be called to the fact that Osborn (1903) erected a subfamily Cryptogoniminae to accommodate his genus but offered no clue as to the family relationships of his newly recognized subfamily. In view of the recharacterization of the Heterophyinae given earlier in this present paper, the genus Cryptogonimus would fall naturally within the subfamily Heterophyinae. Consequently, we propose to reduce the name Cryptogoniminae Osborn to direct synonymy with Heterophyinae.

Heterophyinae: Genus Caecincola Marshall and Gilbert, 1905

(Figure 65)

The genus Caecincola seems to have a very close relationship to the genus Cryptogonimus (Figs. 64 and 65). Its only species, *C. parvula*, displays morphological characters which are closely parallel to the organization of *Cryptogonimus*

chyli. Though neither cirrus nor cirrus sac is present, we have, so far, been unable to demonstrate the presence of a gonotyl. However, the presence of the gonotyl is not essential for inclusion within the family Heterophyidae. Hence we are including Caecincola as a heterophyid within the subfamily Heterophyinae.

Though disagreeing with Odhner (1911:522) and with Poche (1926:165) on the disposition of Caecincola and Cryptogonimus in the system of the trematodes, the present writers are in full agreement with both of the above mentioned authorities in the expression of a belief that Caecincola and Cryptogonimus are closely related. General morphological evidences permit the use of the bond of relationship reflected in general topography of the organs to bind these genera to the Heterophyidae rather than to Acanthostomidae as proposed by Poche.

The short crura, lateral testes, lobed ovary, strong development of the Y-shaped excretory bladder sending its two arms forward to the esophageal region, the limitation of the lateral vitellarian zone, and the method of coiling of the uterus all give evidence of close agreement in the morphology of Cryptogonimus, Caecincola and Centrovarium. Since, added to these characters, Cryptogonimus possesses a gonotyl, its heterophyid nature is established and similar assignment to Caecincola and Centrovarium must follow.

Heterophyinae: Genus Centrovarium Stafford, 1904

(Figure 66)

On the basis of general topography of all the important organs and systems, the genus Centrovarium (Fig. 66) shows a close parallel in detail to the plan of organization found in Cryptogonimus (Fig. 64) and Caecincola (Fig. 65). In much the same spirit that former authorities have sensed the relationship between Cryptogonimus and Caecincola on the basis of general plan of structure (even though the authors have differed radically in the assignment of the paired genera), we feel forced to tie Centrovarium with Cryptogonimus and Caecincola. We assign Centrovarium to the subfamily Heterophyinae.

In Centrovarium the common genital duct which opens through the common genital pore is very short, as in other heterophyids described in this paper. The metraterm and uterus comprise the ventral branch of the fork while the ductus ejaculatorius forms the dorsal branch. This arrangement of the genital ducts seems to be highly characteristic of the Heterophyidae of fishes and adds another point to the list of evidence of unity of the group.

Subfamily Neochasminae Van Cleave and Mueller, 1932

Diagnosis.—Parasitic in digestive tract of fresh-water fishes. Ventro-genital sac median, associated with a single gonotyl. Mouth surrounded by a single crown of spines. Dorsal lip somewhat thickened. Vitellaria lateral, in mid-zone of body. Ovary a pre-testicular, transverse band of follicles. Testes two, spheroidal, at considerable distance from posterior extremity. Uterus chiefly post-testicular.

Type genus.—Neochasmus Van Cleave and Mueller, 1932. Additional genus Allacanthochasmus Van Cleave, 1922.

At the time the genus Neochasmus was described, the authors (Van Cleave and Mueller, 1932) interpreted some of the structures found in that genus to be so distinct from those encountered in the older genus Allacanthochasmus that a subfamily was erected to include Neochasmus alone. Subsequent studies of two species of Allacanthochasmus have confirmed the original belief that Neochasmus and Allacanthochasmus stand as sharply differentiated genera, but have failed to substantiate the belief that the two genera represent different subfamilies. Thus, in spite of the fact that Allacanthochasmus is the older and possibly the more typical genus, the name Neochasminae has been definitely proposed in print and must stand as the designation for this subfamily.

Neochasminae: Genus Neochasmus Van Cleave and Mueller, 1932

(Figures 51 to 54, and 69)

Specimens of the species *Neochasmus umbellus* have been studied in detail to determine the systematic position of the members of this genus. In this study, the validity of the subfamily Neochasminae has been confirmed and the location within the Heterophyidae has been substantiated.

The acetabulum in this genus is deeply submerged (Fig. 54, *ac*) as in Allacanthochasmus and is intimately associated with the genital sinus. The rudimentary gonotyl (*g*) is a surficial modification of the posterior lip of the genital sinus. In this point Neochasmus differs markedly from Allacanthochasmus in form and location as well as in degree of development of the gonotyl. The two species of Allacanthochasmus and *Neochasmus umbellus* constitute a progressive series in the degeneration of the gonotyl (Figs. 67 to 69). In both species of Allacanthochasmus, the gonotyl lies anterior to the genital pore, outside the genital sinus. In this position it is permanently exposed and not susceptible to eversion and retraction as in some other heterophyids. The prominent gonotyl of *A. artus* is replaced by a diminutive surficial papilla in *A. varius* and is still further reduced in Neochasmus. The genital sinus receives the ducts from both ovary and testes and communicates with the exterior through a clearly defined and highly differentiated genital pore anterior to the submerged acetabulum (Fig. 54). Specimens observed in side view demonstrate clearly the presence of a distinct enlargement of the dorsal lip of the oral sucker, though no cecum or posterior appendage to the sucker is present as in members of the subfamily Centrocestinae.

In all points of structure, Neochasmus agrees with the current characterization of the family Heterophyidae except in the form of the ovary. As mentioned by the present writers (1932:24), the follicular ovarian band of Neochasmus does not constitute a palpable quantitative difference from the variable conditions of "globular or slightly lobed" given in Witenberg's diagnosis of the family, but merely extends the range of recognized variation. The ventro-genital complex, the form of the excretory bladder, and the general topography of the entire worm combine to substantiate the claim of heterophyid relationship for Neochasmus.

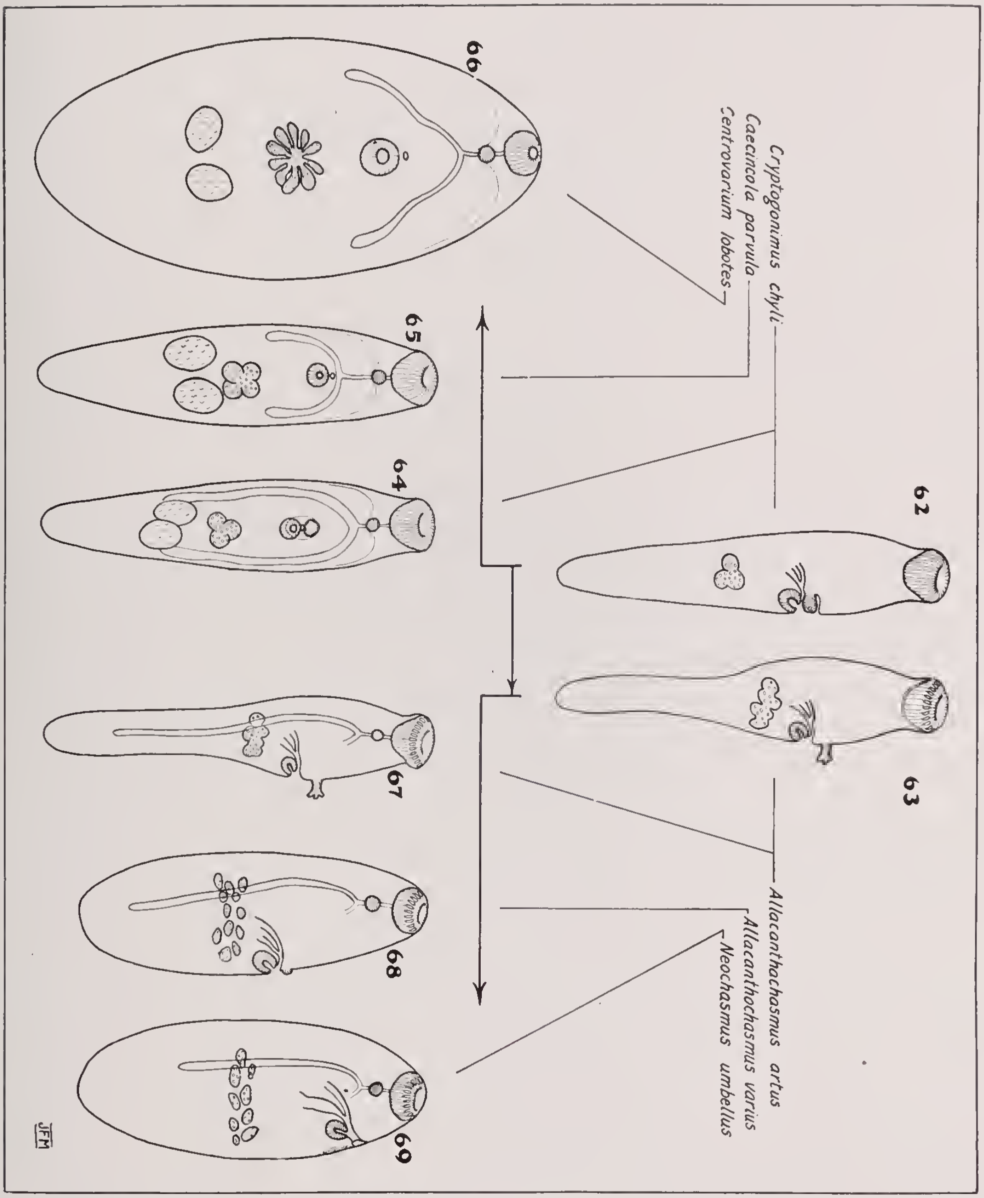
Plate 25. Chart showing evolutionary tendencies in the Heterophyidae inhabiting the alimentary canal of fishes.

Cryptogonimus chyli and *Allacanthochasmus artus* are two forms agreeing in all essential morphological details except in the form and position of the gonotyl and in the fact that the latter species bears a circle of oral spines. About these two stem forms, the heterophyids living in the alimentary canal of American fishes may be arranged in two series showing progressive changes.

In the series consisting of *Cryptogonimus chyli* (Fig. 64), *Caecincola parvula* (Fig. 65), and *Centrovarium lobotes* (Fig. 66), the ovary becomes progressively more lobed and the crura more reduced. The gonotyl characteristic of Cryptogonimus disappears in Caecincola and in Centrovarium but the general resemblance in morphology remains throughout the series.

In the series of forms characterized by the possession of oral spines, the ovary undergoes progressive fragmentation into follicles. Starting with a lobed ovary in *Allacanthochasmus artus* (Fig. 67), the lobes are replaced by separate follicles in *A. varius* (Fig. 68) and in *Neochasmus umbellus* (Fig. 69). In this series also, there is progressive abbreviation of the crura and gradual diminution of the gonotyl until a vestigial structure replaces the functional gonotyl in Neochasmus.

PLATE 25



Cryptogonimus chyli
Caecincola parvula
Centrovarium lobotes
Allacanthochasmus artus
Allacanthochasmus varius
Neochasmus umbellus
62
63
64
65
66
67
68
69
JFM

Neochasminae: Genus Allacanthochasmus Van Cleave, 1922

(Figures 1 to 4, 55 to 61, 63, 67 and 68)

When one of the authors of this paper defined the genus Allacanthochasmus (Van Cleave, 1922:3), no definite family relationship was designated, though comparisons were drawn with certain other genera. Poche (1926:165) in his monographic treatise on the taxonomy of the Trematoda, ascribed Allacanthochasmus to the family Acanthostomidae, evidently founding his action upon statements and comparisons occurring in the original description and upon the opinion of Odhner who believed that neither presence nor absence of oral spines is as safe a criterion of relationship as is general topography of the organ systems. A reinvestigation of the morphology of *Allacanthochasmus varius*, together with studies on a new species, *A. artus*, has revealed several new facts which for the first time provide the grounds for a valid determination of the family relationships of this genus.

Following the preliminary study of the genus Neochasmus, the authors of the present paper were of the opinion that details of the organization of the ventro-genital complex in that genus precluded the inclusion of Neochasmus and Allacanthochasmus in the same subfamily. Consequently a new subfamily, the Neochasminae, was defined in Part I of this report. Subsequent study of the literature has revealed the fact that the differences between Neochasmus and Allacanthochasmus are no greater than similar differences between related genera which Witenberg and other authorities include within the same subfamily concept. In consequence, the genus Allacanthochasmus is assigned to the subfamily Neochasminae.

In the original description of *A. varius*, mention was made of a "crescentic elevation which bears the genital orifice". Recent studies by the present authors, upon living worms and upon serial sections have made clear the true nature of the crescentic elevation mentioned above. Instead of its representing a simple genital pore, it proves (Figs. 60 and 61, *g*) to be the gonotyl of a clearly defined ventro-genital complex. The form of the gonotyl with its crescentic concavity directed anteriorly is clearly figured in the original drawing of the "genital pore" in the original description of the species (Van Cleave, 1922, Fig. 2). The true genital pore (Fig. 61, *d*) is a minute opening between the gonotyl and the ventral sucker, not shown in the original drawing.

In field studies of living specimens of *Allacanthochasmus artus*, the ventro-genital complex has been studied in its varying conditions, and on a number of occasions the gonotyl has been observed in side view. Even in preserved specimens the gonotyl may be seen projecting beyond the body when entire worms are mounted in side view. It protrudes prominently anterior to the ventro-genital sinus near the anterior margin of the acetabulum as a distinct papilla (Fig. 56) bearing a series of five enlargements on its free extremity. The gonotyl of *A. artus* is much more highly specialized than that of *A. varius*. In the latter species, when the gonotyl is viewed from the lateral surface it appears as a simple prominence (Fig. 60) without terminal adornments. In both *A. varius* and *A. artus* we have evidence which seems to indicate that the gonotyl is permanently extruded from the body surface and incapable of retraction within the genital sinus. This is especially well illustrated by *A. artus,* for in all of our whole

mounts the distinctive form of the gonotyl shows clearly and gives no evidence of retraction.

Serial sections in all three planes have been studied to determine the nature of the ventro-genital complex in both species of Allacanthochasmus. All of the sections uniformly give evidence that the ducts of both sexes open by a common genital pore through the common genital atrium lying between the submerged ventral sucker and the gonotyl. In no instance was there any evidence of direct communication between the ductus ejaculatorius and the copulatory apparatus.

As discussed under the genus Neochasmus, there is one point wherein Allacanthochasmus falls short of perfect agreement with current characterizations of the family Heterophyidae, and this is in regard to the form of the ovary. The transverse band of finely divided ovarian follicles is not a wide departure from the lobed ovary of the other heterophyids. This becomes especially obvious when developmental stages are studied. The ovary of *A. artus* is not so minutely divided into follicles as is that of *A. varius*, and we have before us some immature specimens of *A. artus* in which the ovary consists of as few as three lobes. Thus in Allacanthochasmus, ontogeny presents the direct evidence of continuity of the follicular and lobed ovary, for one develops into the other during the lifetime of a single individual.

According to some of the early treatises on the Heterophyidae (Ransom, 1920) the uterus is described as wholly pre-testicular. As pointed out earlier in this paper, later workers have found that uterine development may show extreme variation even within members of the same genus, and consequently this as a limiting character has been omitted from more recent family diagnoses. Accordingly, the extent of the uterus into the posterior extremity in Allacanthochasmus does not discredit the more significant evidences favoring inclusion of this genus in the Heterophyidae.

In sagittal and in cross sections of both species of Allacanthochasmus, the dorsal lip of the oral sucker shows a distinct thickening. On living specimens, this lip overhanging the dorsal edge of the mouth, has frequently been observed as a slight protrusion from the mouth cavity. This condition was not mentioned in the original description of *A. varius*, for its significance was not then understood, but now it furnishes another point of definite agreement with the condition described for some other heterophyids.

The foregoing evidences provide ample grounds for the inclusion of Allacanthochasmus in the Heterophyidae. The proposal of Poche (1926:165) to place this genus in the Acanthostomidae seems wholly indefensible on the grounds of the new evidences here summed up for the first time.

Life cycle

All of the available evidence indicates that the metacercariae of the avian and mammalian heterophyids become encysted in the flesh of fishes after undergoing their parthenogenetic generation in the body of a snail. The complete life history is not known for a single one of the seven genera of fish trematodes discussed in the foregoing synopsis. However, the encysted young of Allacanthochasmus have been found repeatedly in the tissues of fishes which never serve as normal hosts of

the adult flukes. Intact cysts and excysted worms have been removed from the lumen of the digestive system of the same fish host, and in several instances fragments of fish still holding encysted worms were found among the freed cysts. These observations corroborate the supposition that the definitive fish host acquires its heterophyids through the agency of an alternative fish host, as in the avian and mammalian representatives of the Heterophyidae.

SECTION 4. FAMILY RELATIONSHIPS OF THE GENUS MICROPHALLUS WARD, 1901

(Figures 39 to 43)

The position of the genus Microphallus in the system of trematodes has been the subject of prolonged debate. Ward (1901), in the original definition of the genus, recognized it as representing a previously unknown subfamily to which he gave the name Microphallinae. Subsequent workers have expressed many divergent opinions as to the proper allocation of this subfamily. It seems entirely probable that some genera have been added to the subfamily on the basis of superficial resemblances, but without due consideration to fundamental morphological agreement. The type genus alone has been studied in detail. Ward (1901) and Wright (1912) have presented the details of morphology of the type species *M. opacus* in very satisfying details, but isolated observations on other genera have supplied a thin thread of evidence which has been woven into a bond of subfamily unity by other workers interested in establishing the relationships of some other genera which have been ascribed to the Microphallinae. Witenberg has stated that some members of the Microphallinae are provided with a cirrus pouch. If this structure is present in a given genus, it seems to the writers that this fact alone is the best sort of brief for the exclusion of that genus from the Microphallinae. No structure even remotely resembling a cirrus pouch is present in members of the type genus of this subfamily. It seems highly probable that the genera which have come to be considered as related to Microphallus, form, in reality, a composite group not representing a homogeneous subfamily. For this reason, in the present discussion of relationships of the subfamily, attention will be restricted to a consideration of conditions found in the type genus. Some one should restudy the entire group of genera which have been assumed to stand near to Microphallus. Little is to be gained from a reconsideration of the confusing and incomplete descriptions available for these forms in the literature. The new study should be based upon specimens, not upon faulty concepts.

Some measure of the wide disagreement concerning the location of the Microphallinae may be gained from a brief review of the literature. There have been two distinct schools of writers on this subject. One of these has maintained that the subfamily belongs within the Heterophyidae, and the other has adopted the alternative of excluding it, but with diverse solutions as to where it really belongs.

Odhner (1911), Nicoll (1924), Poche (1926) and Fuhrmann (1928) have expressed the definite opinion that the Microphallinae are a subfamily of the Heterophyidae. Stunkard (1929) has shown that the excretory system of Microphallus is more nearly like that of the heterophyids than is that of Cryptocotyle—

a genus very generally admitted as a heterophyid in good standing. However, the indeterminate results of such a study of a single organ system are reflected in the following quotation from Stunkard (1929:265): "If the form of the excretory system is used as the criterion for determining relationships, Microphallus rather than Cryptocotyle should be retained in the family." But in the same paragraph he had previously stated that "The removal of Microphallus from the family Heterophyidae may perhaps be advocated, but the exclusion of Cryptocotyle, I believe, will be hard to justify." Somewhat comparable indecision is voiced by Faust (1929:90) who makes no definite assignment for the Microphallinae, though he tentatively places them in the superfamily Heterophyoidea pending further information regarding the life history.

Opposed to the foregoing point of view stands the united opinion of Ransom (1920), Ciurea (1924), Travassos (1920), Viana (1924) and Witenberg (1929) who either by definite statements rule the Microphallinae out of the Heterophyidae or tacitly do so by failing to make mention of this subfamily in their respective systems of the heterophyids. Witenberg (1929:137) states very definitely that "The genera united in the subfamily *Microphallinae* Ward, 1901, do not belong to the *Heterophyidae,* since they lack a seminal receptacle and some of them are provided with a cirrus pouch."

After a careful study of four species belonging to the genus Microphallus, the present writers are, in principle, in accord with Witenberg's elimination of the members of this genus from the Heterophyidae, but their reasons are somewhat different from those advanced by Witenberg. In the first place, no member of the genus which has come to our attention is provided with a cirrus pouch. The copulatory organ in all members of this genus agrees with the general plan of copulatory papilla such as was originally described by Ward for the type of the genus. This copulatory organ (Figs. 39 and 40, *p*) in all members of the genus consists of a thickening of the terminal portion of the ductus ejaculatorius. This organ is not supplied with a cirrus pouch nor is it on the other hand to be confused with the gonotyl found in many of the heterophyids. So distinctive is this type of cirrus in Microphallus that any genus or species having a cirrus pouch could not be considered as belonging to the same family and must be excluded from the Microphallinae. At the same time the cirrus of the true Microphallinae is so distinctly different from the copulatory apparatus of the heterophyids that on this fact, with the lack of a seminal vesicle and the nature of the genital pore as contributory, we base our argument for sharp separation of Microphallinae from Heterophyidae.

In every one of the seven genera ascribed to the Heterophyidae in this paper, the ducts from the gonads open into the genital sinus by way of a common genital duct. There is thus a single genital pore in all of the Heterophyidae of fishes discussed in this report. Contrary to this arrangement stands the condition found in Microphallus (see Plate 22) wherein the two genital ducts open independently in a shallow genital sinus (Figs. 39 to 42).

Ward (1901) made detailed studies of the male genitalia of *M. opacus* and was able to secure specimens fixed in copula, so there can be no doubt as to the functional relations of the cirrus and the genital pore. The present writers have studied the same species and in addition have investigated *M. ovatus* (Plate 22)

wherein the copulatory organ was found to be in intimate agreement with Ward's description of *M. opacus*. In two other species which the present writers have described from fishes of Oneida Lake, New York, the general topography of the genital organs is the same, but the seminal vesicle is highly modified and the copulatory papilla is much more elongated than in *M. opacus* and *M. ovatus*. All four of the species that have been investigated bear out the conclusion that the Microphallinae stand as a sharply isolated group.

Travassos (1920) elevated the Microphallinae to family rank and in this was followed by Viana (1924). In this elevation, the present writers concur. The genus Microphallus is distinctly and incompatibly different from the Heterophyidae. The degree of separation warrants the recognition of a family Microphallidae to include the genus Microphallus. Until the detailed morphology of Levinseniella, Spelotrema, Spellophallus, Monocaecum, and Maritrema has been determined as compatible with that of Microphallus, these genera should be excluded from the Microphallidae, though Poche (1926:151) has attempted to relate them to the subfamily Microphallinae.

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TRICHODINA RENICOLA (MUELLER, 1931), *A CILIATE* PARASITE OF THE URINARY TRACT OF *ESOX NIGER*

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CONTENTS

INTRODUCTION

On numerous occasions the chain pickerel (*Esox niger*), in Oneida Lake, has been found to bear in its urinary tract a peritrichous ciliate which was at first taken to be a species of Cyclochaeta, and named *Cyclochaeta renicola*. The name, with a brief description, was published in an abstract in the Journal of Parasitology, December, 1931, in the section "Abstracts of Papers Contributed for the Seventh Annual Meeting of the American Society of Parasitologists, New Orleans, La., December 29, 30, and 31, 1931". It was originally planned to present a paper on this parasite before the meetings of the Society, but at the last moment the author was unexpectedly prevented from attending, so that the paper was not read.

Subsequent study of the protozoan has disclosed the fact that in the original description it was erroneously allocated in the genus Cyclochaeta, but belongs properly in the closely related genus Trichodina. Its correct name therefore becomes *Trichodina renicola* (Mueller, 1931). The present paper gives a more extended description of this parasite, with a discussion of its systematic position, and its host relationships.

SYSTEMATIC POSITION OF T. RENICOLA

The genus Trichodina is a natural relative of two closely similar genera, Cyclochaeta and Urceolaria. There is no general agreement concerning the exact systematic position of these forms. Fulton, 1923, following the example of Wallengren, 1897, unites the three genera in the family Urceolariidae of Stein. The Urceolariidae, according to this classification, form the third family of the Order Peritrichida.

Calkins, 1926, on the other hand, reduced the group to subfamily rank, the Urceolariinae, under the family Vorticellidae, following Doflein and Minchin. This disposition of the group is, however, objectionable. The Urceolariidae form a natural group sufficiently well characterized and set off to justify their receiving equal rank with the Vorticellidae. Furthermore, discrepancies appear in Calkins' key. On page 411, under Peritrichida, at 2, he has as second alternative "*Not parasitic,* posterior end not flexible — Family 3. Vorticellidae." He then places under the family Vorticellidae the subfamily Urceolariinae, made up almost entirely of *parasitic* forms. Moreover Calkins suppresses the genus Urceolaria, probably with the idea that it is synonymous with Cyclochaeta. This also seems unwarranted, since, as described by various authors, Urceolaria is clearly set off from Cyclochaeta by the absence of hooks from the corona.

Kudo, 1931, also omits Urceolaria and places the two genera Cyclochaeta and Trichodina in the family Trichodinidae, Claus, making this the first family of the Peritricha.

Inasmuch as the genus Urceolaria has distinctive skeletal features, it seems more logical to retain it as a separate concept. For this reason the system followed by Fulton, 1923, still seems to be the best. This is given here.

Family Urceolariidae, Stein (3rd family of *Peritrichida*).

Genus Urceolaria: With a ring of cirri anterior to posterior girdle of cilia, and without hooks on the denticulate ring.

Genus Cyclochaeta: Like *Urceolaria,* but with hooks on the denticulate ring.

Genus Trichodina: Like *Cyclochaeta,* but without cirri.

In this analysis I omit the characters of the peristome given by Fulton, 1923. These are not constant for the genera and when used in a key result in confusion. The reader is referred to Fulton's paper, which gives an excellent review of the family, and an account of Wallengren's fundamental work, published in Swedish, and hence inaccessible in the original to most English-speaking zoologists.

URCEOLARIIDAE PREVIOUSLY DESCRIBED

A number of different Urceolariidae have been described. With the exception of the Trichodina reported by Rosseter and Fulton from the urinary tract of amphibia, most of them live as ectoparasites, or ectocommensals, on the surface of various animals. Only a few of them will be mentioned here.

A review of the different species is given by Fulton, 1923, and a number are also mentioned by Reynolds, 1930. Many of the Trichodina reported have been found, or suspected to be, synonymous with *Trichodina pediculus* Ehrenberg. In company with several other Trichodinae this species is apparently without any definite host specificity, and has been reported from such widely different sources as the skin and gills of urodele larvae, and the surface of fresh-water hydroids. Fulton, 1923, described another species, *T. urinicola*, from the urinary bladder of a toad. Fulton recognized this species as the same as one which Rosseter, 1886, had described from the kidneys, urinary bladder, urinary ducts, and testes of *Triton cristatus*. Structurally this species is close to *T. pediculus*, but Rosseter showed that the *T. pediculus* from the surface and gills of amphibians would very readily infect Hydra, proving its identity with *T. pediculus*; whereas the form from the bladder could not be induced to infect the polp, but recoiled from it.

The generic allocation of several of the Urceolariidae is in flux. Thus Fulton lists *Urceolaria mitra* (von Siebold), from planarians; *Urceolaria patellae* Cuenot, from gills of mollusca; *Cyclochaeta scorpenae* Fab.-Dom., from gills of fish; and *Cyclochaeta synaptae* Cuenot, from echinoderms. Whereas Reynolds, 1930, refers to all these species as Trichodina. There is, however, no adequate reason for this simplification, and until further studies are made Fulton's usage should be followed.

Cyclochaeta domerguei Wallengren has been reported from European fish. Frequent references to Cyclochaeta occur in the literature of fish culture, usually without any designation of species. It is doubtful in most cases whether the material dealt with is Cyclochaeta or Trichodina, for in ordinary observation the difference between the two would probably not be noticed. Plehn, 1924, refers to several Cyclochaeta encountered in fish culture in Germany, giving diameters and number of hooks in the horny ring. In her description she mentions "Ein Kranz langer Wimpern, . . . ausserdem sind plumpere, breitere Cirrhen vorhanden." In her drawing, however, there is no indication of a row of cirri, and the posterior crown of cilia is erroneously made to turn in at one side after the fashion of the adoral spiral.

Hofer, 1904, on the other hand, reports *Cyclochaeta* on fish in Germany, and gives a figure (after Moroff) of *C. domerguei*, in which the row of posterior erect setae are correctly shown. Some distance anterior to these appear the cilia of the oral groove.

Davis, 1929, mentions Cyclochaeta as occurring commonly on American trout. He figures a form with 23 hooks in the denticulate ring, but with no cirri, and in his description he mentions the posterior girdle of cilia and the adoral spiral, but makes no reference to cirri. Thus if his description is correct the form is a Trichodina. The present writer has collected material from western trout, somewhat similar to the form figured by Davis. This species has 29 to 30 hooks in the skeletal ring, and was at first thought to be Cyclochaeta, but after careful study no cirri are discoverable. It is 0.120 mm. in diameter (over twice the diameter of *C. domerguei* — 0.055 mm.), and the process of fission and rebuilding of the skeletal ring is similar to that described by Wallengren and Fulton for Trichodina. This species has not been sectioned, and so it is not possible to state with certainty

that cirri are absent. However, they appear to be lacking in observation of the entire animal, and in all probability this is a species of Trichodina, ectoparasitic upon trout, which has hitherto been mistaken for a Cyclochaeta.

Diller, 1928, published a very excellent paper on binary fission and nuclear phenomena in a species of Trichodina found on anuran tadpoles. He was unable to identify his form with any previously described species, and left it undetermined.

In very recent years a number of species of Trichodina have been described from various hosts by Ariake (1929), da Cunha and Pinto (1928), Fantham (1930), and Ibara (1931).

With the exception of *Trichodina fariai* these are either from the exterior of various fishes, or from the urinary system of amphibia. Da Cunha and Pinto's species, *Trichodina fariai,* was from the intestine of a marine fish from the coast of Brazil, and hence, although endoparasitic in a fish, could not be the same as *T. renicola.* Fantham described a number of species ectoparasitic on South African fishes, and one from the urinary system of a toad. Ariake lists a number of new species from goldfish in Japan. Ibara's species was from the urinary bladder of a salamander in Japan. None of these could be synonymous with *T. renicola* from *Esox niger* in Oneida Lake.

T. renicola cannot be identified with any previously reported form known to the writer, but in general aspect it comes closest to the form worked on by Diller. From this it differs in certain respects which will be emphasized later on.

ANATOMY OF TRICHODINA RENICOLA

This species occurs as an endoparasite in the urinary bladder and ureters of the pickerel, *Esox niger,* in Oneida Lake. The anterior surface (the side away from the sucking disc) is strongly arched, but less so than in most other species of Trichodina. There is no suggestion of the hour-glass shape of *T. pediculus,* or of the barrel-shape of *T. urinicola.* Normally *T. renicola* has the form of a small hemisphere (Figs. 2, 3, 8), with a diameter of about 0.080 mm. Small specimens have been observed which were only 0.070 mm. in diameter, and large ones as much as 0.096 mm.

The adoral spiral of cilia, or peristome, consists of a well defined groove passing in a helix around the anterior surface in a right handed direction. The axis of this helix corresponds to the vertical axis of the animal. Two rows of long cilia spring from the edges of the adoral groove. At their bases these cilia are fused so as to form two continuous parallel membranelles. At their distal ends, however, the cilia are free. At its lower (outer) end the adoral groove makes a sharp turn and swings into the vestibulum. As it descends into the vestibulum, the ciliated groove makes a complete spiral circuit of its wall. The membranelles pass along the groove clear to the bottom of the vestibulum. The gullet arises from the bottom of the vestibulum at a slight angle, and passes inward toward the center of the animal. A large contractile vacuole lies alongside the vestibulum between the ends of the macronucleus. It opens into the vestibulum by a connecting duct, which usually shows up very clearly in stained specimens. In other species this vacuole is known to pulsate, sluggishly in *T. urinicola,* but rapidly, at intervals of 10 to 12

seconds, in *T. pediculus*. *T. renicola* was studied chiefly from stained and mounted material, and the interval of pulsation in its contractile vacuole was accordingly not observed.

The macronucleus of *T. renicola* has the shape of a horse-shoe, parallel to the plane of the sucking disc, with the ends lying close together, separated by the vestibulum and contractile vacuole. It consists of a basophilic ground substance, of finely granular nature, containing numerous vacuoles. Within the vacuoles lie chromomeres of a refractile, homogeneous material, having less affinity for stain than the rest of the nucleus (Fig. 5). As in *T. pediculus,* the micronucleus in *T. renicola* appears to be embedded in the wall of the macronucleus, near the end that approaches the vestibulum (Fig. 4); but in many specimens the micronucleus could not be found.

The cytoplasm consists of a thin, condensed outer layer, or pellicle, and a loosely granular, highly vacuolated endoplasm. Myonemes were not observed.

The most remarkable feature of the animal is the attachment surface or sucking disc. This consists of a central exoskeleton or ring, a girdle of cilia, and a marginal lip or velum. The velum in *T. renicola* consists of a marginal fold of cytoplasm, having an outer pellicle, and finely granular contents, with a greater affinity for eosin than the rest of the cytoplasm. The thickness of the velum varies greatly in different individuals. In some it is a thin compressed flap, whereas in others it is so thick that one would incline to regard it simply as the edge of the body, instead of a specialized structure. The velum in *T. renicola* is the least specialized part of the sucking disc, and is much thicker than in most species of the genus.

The skeletal ring consists of two parts — an upper (anterior) striated ring (the "Ringband") and the denticulate ring, or corona. The relationship of these parts is shown in drawings, figures 6 to 10. The striated ring is composed of narrow radial bars fused into a circular plate with a round central aperture. Each bar forks about midway into an upper (anterior) branch, and a lower (posterior) branch. The ends of the upper branches form a continuous band around the circumference of the animal, and support the posterior groove of cilia. These cilia will be discussed later. They lie just under the velum. A second narrow flap of protoplasm, somewhat similar to the velum, but smaller, fills in the space between anterior and posterior branches of the radial bars.

The corona consists of numerous segments, usually 56, having the shape of cones, fitted into each other to form a continuous circle. From the edges of the cones, toward the ventral side, paired, thin processes arise, which extend inward and outward. The outer process extends centrifugally in a graceful curve, and is called the hook. Its inner process, or ray, passes in a straight line centripetally, and terminates opposite the inner edge of the striated ring. Both hooks and rays are joined by a thin, interstitial membrane (Fig. 7). Inwardly the pellicle of the animal is continuous with the edge of the striated ring. From this edge it curves downward and joins the inner ends of the rays. Ventrally the pellicle is continuous with the interstitial membrane of the rays, and passes inwardly over the large plug of protoplasm which projects downward through the aperture of the striated ring to the level of the rays. An empty chamber is left between the striated ring

and the corona (Figs. 6, 8, 9). A narrow membranous flap with free edge curving downward and inward, arises from the lower edge of the striated ring where this edge is joined to the hooks. This membrane has been rather inadequately designated by Wallengren as the border ("Saum"). It is an important structure in that it forms the functional edge of the sucker (Figs. 7, 9).

The posterior girdle of cilia in *T. renicola* has the same peculiar structure which was described by Wallengren for Urceolaria. It consists of a series of membranelles, each membranelle made up of ten or twelve cilia standing in line to form a flat oblong plate set on end. The cilia fringe out at the free end of the membranelle. At their bases the membranelles are attached to their ring of origin in oblique fashion, like the teeth on a worm-gear wheel. Erect bristles, or cirri are completely lacking, and hence the necessity of transferring the species from Cyclochaeta, where it was originally placed, to the genus Trichodina.

COMPARISON WITH OTHER SPECIES

T. renicola differs from most species of Trichodina in the more compressed, rounded body form. *T. pediculus*, and related types, have a tall body, with the adoral groove forming a large circle on the upper edge, delimiting a flat anterior surface which is even greater in diameter than the sucking disc. They have in general a "flower pot" shape. *T. steini* has a more elevated body with a sharper apex. *T. urinicola* has a pronounced barrel shape, with the top end rounded off. It has a small sucking disc, and greatest diameter in the middle of its height. It is about twice as tall as the diameter of its sucking disc. *T. renicola* comes nearest to *Trichodina sp.* described by Diller, 1928, on tadpoles. Both species have the same hemispherical shape; however, Diller's form was much smaller — only 0.035 mm. in diameter — whereas *T. renicola* is about 0.080 mm. in diameter. *T. renicola* has a larger number of hooks in its denticulate ring than any other species of the Urceolariidae known to the present writer. *T. pediculus* has 24 to 26 denticles in its corona, and the same limit applies to related forms. *T. urinicola* has 28 to 36 hooks in its ring. Diller's Trichodina had 15 to 24 denticles in the corona with 21 as the mode. *T. renicola,* however, regularly has 56 hooks in its ring. In the genus Cyclochaeta the number is usually less than thirty.

BINARY FISSION IN T. RENICOLA

As is usual in the Urceolariidae, this species reproduces by binary fission, with two offspring of equal size resulting. The skeletal ring divides transversely in the process and the two ends join. For a short time, such young individuals have a corona with only half the normal number of denticles, and the denticulate ring lies near the center of the striated ring. Individuals of this sort were found for *T. renicola*, but the subsequent stages in the assumption of the adult condition were not observed. It has been shown, however, in other species, that a second ring of denticles forms *de novo* peripheral to the smaller, inherited ring, and this second ring has from the first the normal number of denticles for the species. The writer has observed this process in the above mentioned species of Trichodina (?) from the trout. There is no reason to doubt that it is repeated in the usual

manner for *T. renicola*. As the new ring assumes the final form the smaller ring is resorbed.

Immediately after fission the macronucleus is shorter than in the adult, forming scarcely a half circle. It elongates with growth until the final proportions are reached. A young *T. renicola*, immediately after fission, with a short macronucleus, and half the normal number of denticles in its corona, is shown in figure 5. The new ring of denticles has not yet begun to form.

TECHNIQUE

The material forming the basis of this study was fixed by opening infected bladders and dropping the contents into hot Bouin's fluid. After washing, the protozoa were stained in Ehrlich's hematoxylin and mounted *in toto*. Entire bladders, known to be infected, were dropped whole into hot Bouin's, and later the contents were removed, or the bladders were sectioned without opening. Pieces of kidney were fixed by various methods, and later sectioned to study the parasites in the ureters. For sections, ordinary hematoxylin and eosin were found to give good differentiation. The corona and striated ring have a strong affinity for eosin and stand out with great clearness after this procedure.

Other authors have tried fixing smears on slides and staining as in blood work, but this procedure did not appear necessary or suitable for purposes of this study, and was not used.

HOST RELATIONSHIPS

T. renicola appears to be very specific for its host, *Esox niger*. So far, the parasite has been observed only incidentally, while making a survey of helminth parasites. After the date of initial discovery, December 26, 1930, twelve pickerel were examined at different times up to the present date, and only two failed to harbor the organisms. The closely related *Esox lucius*, however, was not infected, even when taken from the same habitat and in the same net with infected *Esox niger*.

Outwardly the infected fish appeared normal. The intensity of the infection varies from a sparse population of Trichodina at the neck of the urinary bladder, to a very heavy bladder infection in which the protozoa are literally swarming. When such a bladder is opened, the contents have a creamy appearance due to the enormous numbers of Trichodina present. In such heavy infection the ureters and kidneys are found to be involved. The parasites invade the ureter and its branches, ascending these ducts as far as possible until the diameter of the tubes becomes too small to allow further ascent to the Trichodinae. In sections they can be seen at times literally packed in the ureters, not only lining the walls, but lying on top of each other and free in the lumen of the tube.

PATHOLOGY

Little is known about the pathological effects of Trichodina or Cyclochaeta infection. In very heavy infections of small fish, Cyclochaeta may cause the death of the host. Hofer states that their presence in large numbers causes an inflamma-

tion of the mucous epithelium, with overproduction of slime, sloughing of cells, and the appearance of inflamed or cloudy patches. Several factors may enter to produce injury to the host. In the first place, the mere presence of such forms in numbers on the gills or integument may interfere with gaseous exchanges to such an extent as to cause suffocation of the host. In the second place, substances may be given off by the Trichodinae which have a toxic effect upon the host. In the third place, a certain amount of direct injury is probably done to the host epithelium by the action of the sucking disc of the parasite. The exact extent of this mechanical injury is uncertain, but, it would appear that Trichodina is capable of considerable power of suction. Hofer states that due to the action of Cyclochaeta, groups of epithelial cells are gradually loosened and dislodged. In sections of bladders and kidneys of Esox, with Trichodina, the Trichodinae are seen in many cases closely applied to the epithelial wall. The sucking disc can be very strongly activated, the protoplasmic plug, which passes through the center of the exoskeleton, being drawn upward after the manner of a piston, lifting the inner edge of the skeletal ring with it. In this manner a deep sucking cup is formed and the body assumes the shape of a bell. Animals with this shape can be seen applied to the walls of the urinary tract, with the epithelium bulging upward into the bell. The edge of the sucker fits into a deep groove in the host tissues. Whether this effect is the result of sucking action, or whether such animals merely chanced to settle down upon a convenient elevation of the epithelial wall cannot be stated. However, definite areas of laceration and desquamation of the epithelial cells can be found which can only be attributed to the mechanical effects of the parasite, and at times clumps of such dislodged and disintegrating epithelial cells lie free in the lumen of the ureter.

The glandular part of the kidney appears normal, the size of the Trichodinae preventing the parasite from entering the tubules. There would appear to be some possibility of blockage of the ureter from the large number of parasites present, but if this ever occurs it has not been observed.

Fulton was inclined to attribute the moribund condition of a toad found infected with *T. urinicola* to the presence of the enormous numbers of the parasites in the urinary bladder. In spite of the occurrence of mechanical damage to the urinary epithelium of the host in *T. renicola* infection, the amount of injury does not seem sufficient to cause serious consequences. However, it is possible that toxic products given off by the parasites are absorbed by the host with detrimental effects. Nothing is known about this aspect of the problem. Diller noted that tadpoles bearing a heavy infection of Trichodina on their outer surfaces were smaller than tadpoles with a light infection. He was hesitant, however, about attributing any stunting effect to the presence of the parasite.

Upon superficial examination, infected kidneys and bladders appeared normal.

TRANSMISSION OF THE PARASITE

Since both external and endoparasitic forms of Trichodina are known the transmission of the organism from fish to fish would appear to be capable of easy explanation. A brief period of ectoparasitic existence with transfer and resumption of the endoparasitic habitat through the cloaca, would seem to be a

plausible hypothesis. Actually, however, the problem is probably not so easy. Nearly all the endoparasitic protozoa offer problems in the question of their transmission, which seem opposed to a simple solution.

Rosseter, 1886, demonstrated conclusively a difference in reaction between closely similar Trichodinae living on the outside of and within the urinary bladder of *Triton cristatus.* The ectoparasitic species was shown to be the same as *T. pediculus,* commonly infecting Hydra as an ectocommensal. The endoparasitic form, however, did not live upon the external surface of its salamander host, and recoiled from Hydra. This latter species is regarded by Fulton, 1923, as identical with his *T. urinicola.* Fulton found *T. urinicola* incapable of living outside the urinary bladder of its host. It is an endoparasitic organism, apparently unable to establish even a brief external residence. He further mentions that numerous other amphibians which had been kept in the same aquarium with the infected toad were found negative. If the parasite were easily transmitted one should expect that under close proximity all of the associated animals would have become infected. The fact that they were not could not be attributed to host specificity, for this Trichodina, also reported from *Triton cristatus,* would appear to have a wide choice of hosts.

Careful search has so far failed to reveal any Trichodina living ectoparasitically upon pickerel infected with *T. renicola.* When removed from the bladder into lake water the life of the organism is very brief. It swims about actively for a short period, but rapidly swells up (endosmosis?), and within two or three minutes dies and disintegrates. That the parasite does pass from fish to fish, and very efficiently, however, is indicated by the high incidence of infection in pickerel in Oneida Lake.

No other Trichodina has been found by the author in Oneida Lake, and numerous examinations of fish gills for ectoparasites have failed to reveal either this genus or Cyclochaeta. That *T. renicola* is widely distributed in Oneida Lake, however, is shown by the finding of infected pickerel at both ends of the lake — in Big Bay, and Fish Creek, twenty miles apart, as well as in the Cleveland harbor, in about the center of the north shore of the lake.

A study of all phases of this disease is planned in the near future.

Trichodina renicola appears to be the first species of the family reported from the urinary system of a fish. It offers a close parallel to the form found in the urinary tract of Amphibia, and extends this type of parasitism into another Class of the Vertebrates.

T. renicola, however, is unique in its narrow host specificity. Although hundreds of fish, of about thirty different species, from Oneida Lake, have been examined by the present writer for parasites, Trichodina has never been found in any except *Esox niger.* This is quite a contrast to the habits of *T. urinicola,* which apparently infects indifferently a number of diverse species of amphibians. Diller, likewise, found his Trichodina abundantly present on all species of tadpoles examined.

A slide containing numerous stained specimens of *T. renicola* has been deposited in the U. S. National Museum, as cotype material of the species.

SUMMARY

1. *Cyclochaeta renicola* Mueller, 1931, is removed to the genus Trichodina.

2. The species is described. It appears to be a valid form, differing from others previously reported in the large number of denticles (56) in its corona, as well as in other characters.

3. The parasite is found in the urinary system of *Esox niger,* causing some mechanical injury; but apparently no serious consequences result to the host.

4. This is the first Trichodina described from the urinary tract of fish.

5. *T. renicola* differs from *T. urinicola,* reported from the urinary tract of various amphibia, in its specificity for a single host, *E. niger.* This fish is generally infected in Oneida Lake.

6. The mode of transmission of the parasite is unknown.

Plate 26. Superficial anatomy of *Trichodina renicola.*

Fig. 1: Cross section of ureter of *Esox niger,* showing Trichodina in lumen and attached to wall. The surrounding kidney tissue not shown.

Fig. 2: Cluster of Trichodina as removed from wall of infected bladder, after bladder was fixed whole. The parasites are so abundant that they crowd each other closely for attachment room on the wall of the bladder, and consequently rest on top of each other several layers deep.

Fig. 3: View of a *Trichodina renicola* from the side, looking into the concavity of the sucking disc, showing form of the animal and arrangement of the parts. Frequently the parasites are more convex than this specimen.

Fig. 4: View of a specimen from above, looking at the anterior surface. The helical adoral groove shows clearly. Relationship of the macronucleus, gullet, and contractile vacuole to the vestibulum are also shown.

Fig. 5: A young individual just after fission, seen from below. The corona has only half the normal number of denticles, and the macronucleus is shorter than in the fully grown specimens.

Explanation of plate

Figures 3 and 4 drawn free hand. All others with camera lucida and Leitz microscope. Figure 5, with 1/12 oil immersion objective and 16x ocular. Fig. 4, with 1/12 oil immersion objective and 8x ocular. Figure 1 with 3x objective and 16x ocular. Figure 2 with 6x objective and 8x ocular. Figure 3 with 6x objective and 16x ocular.

Abbreviations

ao—adoral spiral of cilia
b—border ring of sucking disc
eu—epithelial wall of ureter
g—gullet
m—mouth
mn—micronucleus
mu—muscular wall of ureter
n—macronucleus
pc—posterior girdle of cilia
rb—striated ring, or ring band
sr—denticulate ring, or corona
t—Trichodina within ureter
v—velum
vac—contractile vacuole

Plate 26

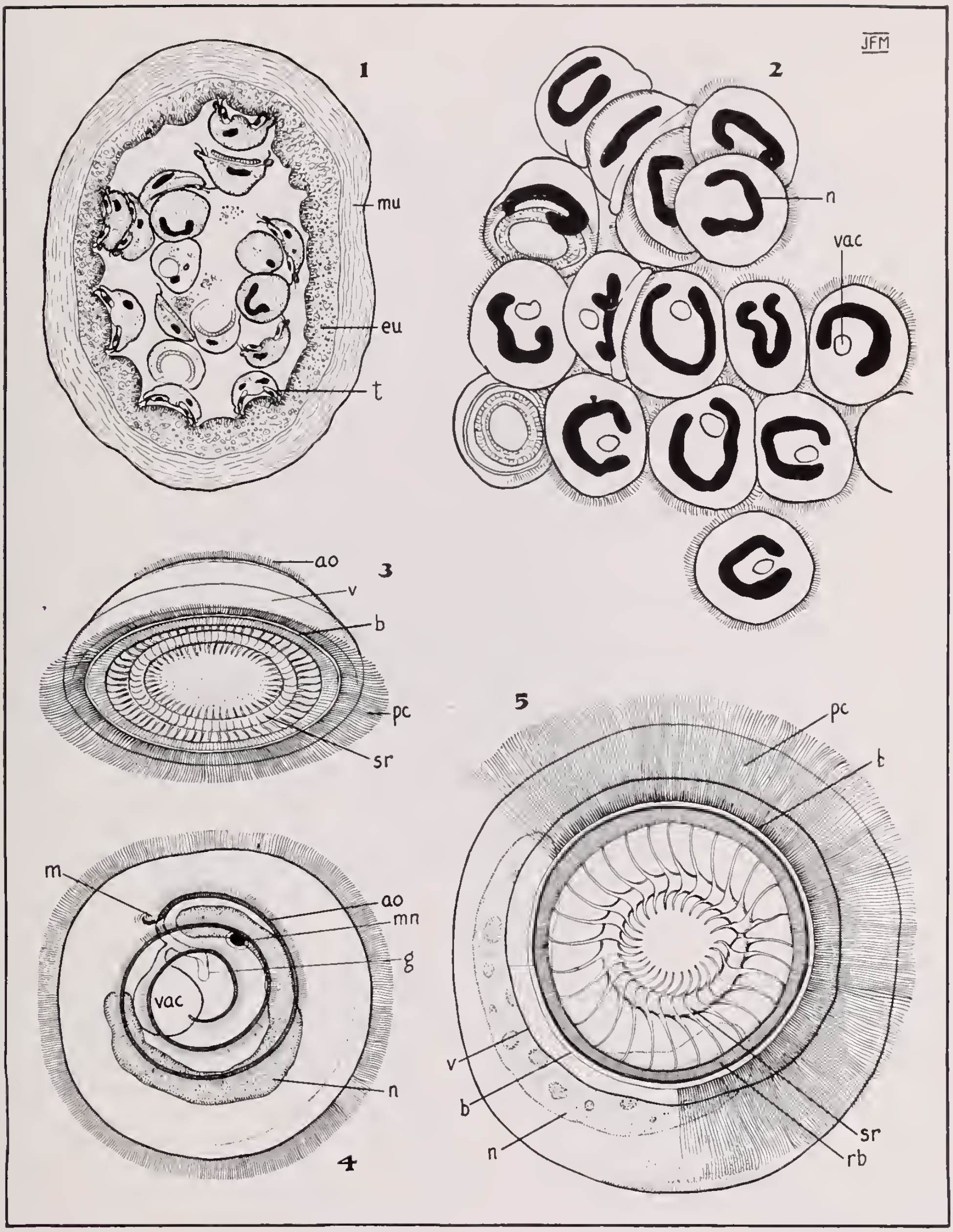


Plate 27. Detailed anatomy of *Trichodina renicola.*

Fig. 6: Partly diagrammatic drawing showing the relationship of the parts of the exoskeleton. The upper arms of the ring bars are cut away at right to show the shorter bars at the lower level. Ring band partly left out to reveal the corona below. The denticles of the corona are shown partly in surface, and partly in cut-away view, to explain their relationship.

Fig. 7: Schematic diagram showing parts of exoskeleton and their arrangement.

Fig. 8: Section of *Trichodina renicola* through vertical axis. The vestibulum with the spirally winding end of the adoral groove shown at right. Somewhat schematic in this region in order to show gullet and vestibulum in same view.

Fig. 9: Detail of parts shown in above, drawn from a number of specimens.

Fig. 10: View of exoskeleton seen from above. Bars of ringband indicated only as far as edge of corona, except for small sector at left. Actually they should cover entire corona in this view (dorsal), as far as inner ends of the rays. Only 53, instead of the usual 56, denticles in this specimen.

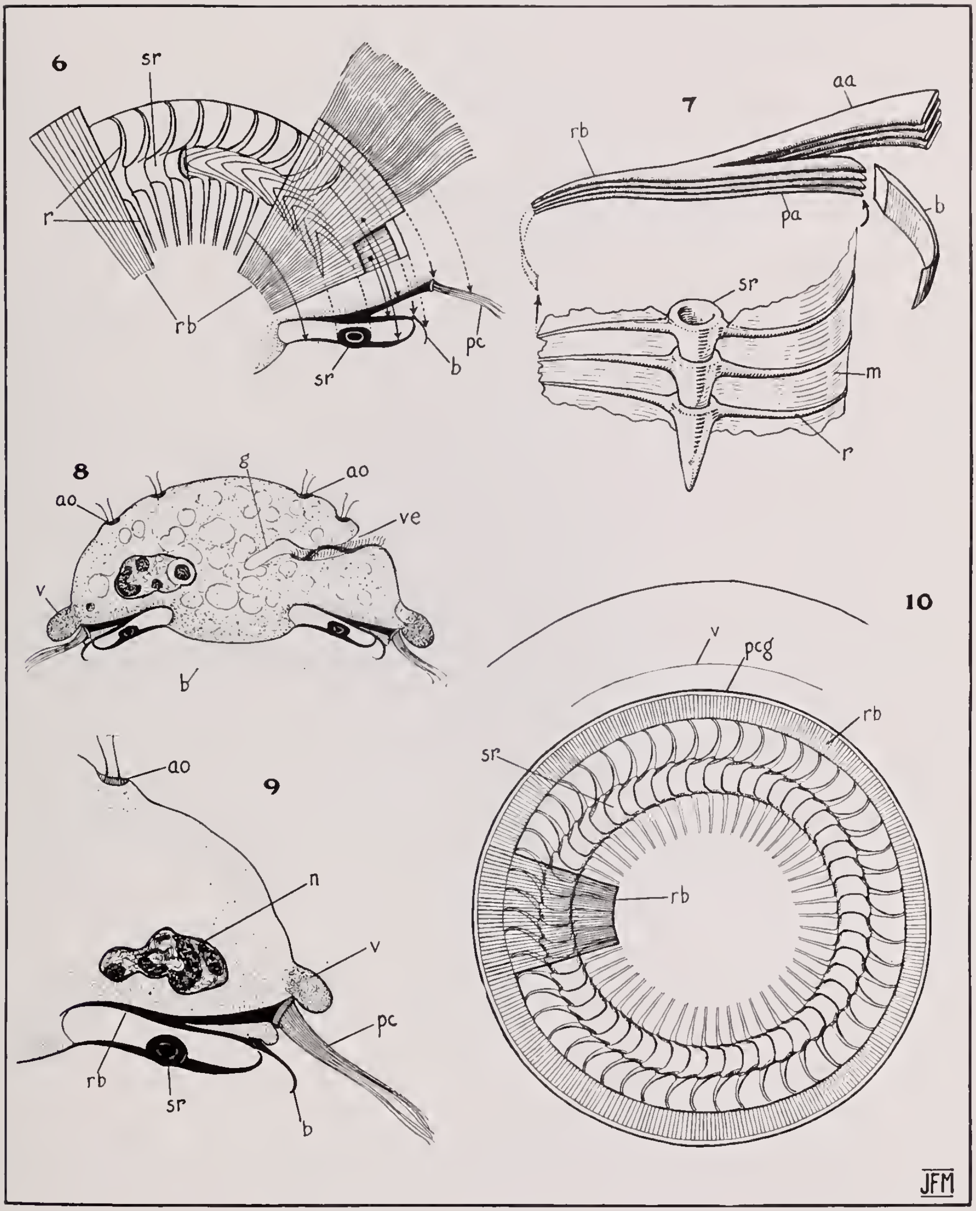
Explanation of plate

All figures drawn with camera lucida and Leitz microscope. Figures 6 and 10, with 1/12 oil immersion objective and 16x ocular. Figure 8, with 1/12 oil immersion objective and 8x ocular.

Abbreviations

aa—anterior arm of striated ring bars
ao—adoral spiral of cilia
b—border membrane of sucking disc
g—gullet
m—mouth
n—macronucleus
pa—posterior arm of striated ring bars
pc—posterior girdle of cilia
pcg—groove of origin of posterior girdle of cilia
r—hooks and rays of denticulate ring
rb—striated ring, or ring band
sr—denticulate ring, or corona
v—velum
ve—vestibulum

PLATE 27


6
sr
r
rb
pc
b
sr
7
aa
rb
pa
b
sr
m
r
8
g
ao
ao
ve
v
b
9
ao
n
v
pc
rb
sr
b
10
v
pcg
rb
sr
rb
JFM

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